Impacts of Forest Degradation and Oil Palm Conversion on Ecosystem Structure and Functioning in Sabah, Malaysian Borneo

Dissertation

zur

Erlangung der naturwissenschaftlichen Doktorwürde

(Dr. sc. nat.)

vorgelegt der

Mathematisch-naturwissenschaftlichen Fakultät

der

Universität Zürich

von

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Zürich 2014

Contents

Summary

In this thesis, we investigate the effects of forest degradation and habitat change on vegetation structure and ecosystem function of Borneo forest. We sample the old growth, moderately logged and heavily logged forest to examine consequences of forest degradation. In order to observed the effect of forest habitat change to oil palm, we sampled oil palm plantation, in which palm were planted between 2000 and 2006.

In Chapter 1, we highlight the research rationale in forest degradation and habitat change of tropical forest. Many studies on tropical forest ecosystems had discovered threats and opportunities to improve biodiversity in degraded forests and agricultural landscapes. The complexity of biodiversity and competition of land use has initiated several biodiversity experiments worldwide. Indeed, sustainable management and comprehensive planning in logging operation can minimize the loss of biodiversity. Integrated land use of forest habitats into existing agricultural areas may improve the biodiversity and ecosystem function.

In Chapter 2, we quantify tree density, basal area, coarse woody debris (CWD) volumes and total aboveground carbon (TAGC) stocks in old growth forest and degraded forests that had been moderately logged and heavily logged, as well as in oil palm plantation. We find that forest degradation has affected the forest structure and decreased TAGC stocks. Tree density, basal area, CWD volumes and TAGC stocks decreased with increased of logging intensity. A positive correlation between TAGC stocks and basal area was observed across forest types but for a given basal area oil palm has lower TAGC stock due to its low C density. Our results indicate that forest degradation and habitat change decreased the vegetation structure and reduced the TAGC stocks.

In Chapter 3, we evaluate effects of forest degradation and habitat changes on annual litterfall production and leaf litter carbon (C) and nitrogen (N) concentration and C:N ratio. We find litterfall production varied across sites but was indistinguishable among forest types and lower in the oil palm plantation. The oil palm leaf produced the lowest C and highest N concentration, and thus lower C:N ratio compared to mixed leaf litter across forest types. These results indicate that forest degradation has not had a detectable large impact on litterfall production and C and N concentration, but conversion to oil palm plantation causes a shift to vegetation with very different properties.

In Chapter 4, we investigate the effects of forest degradation on the canopy cover and seedlings dynamics across forest types. We find that seedlings in sampling sites belonged to 63 families, where species of the Fabaceae, Euphorbiaceae and Annonaceae appear in most of forest types. The Dipterocarpaceae is dominant in the unlogged forest. The vegetation cover of trees is higher in unlogged forest than in moderately logged forest and heavily logged forest. Meanwhile, vines, and herbaceous plants are more common in heavily logged forest. Seedling density was lower in heavily logged forest. However, seedling basal diameter sizes were not significantly different across forest types. Variance components analyses indicate that species identity is important for seedling natural recovery assessment.

In Chapter 5, we discuss a main finding reported in Chapter 2, 3 and 4. We highlight ideas for possible future research to advance our knowledge into forest degradation and habitat change. We suggest several management approaches that may improve biodiversity in degraded forest and oil palm plantation. The results of this study will be an important part of the pre-fragmentation initial conditions of the SAFE Project. All of these are crucial to support the biodiversity conservation efforts in degraded forest and to understand the consequences of habitat change in tropical forest of Southeast Asia.

Zusammenfassung

In dieser Arbeit untersuchen wir den Einfluss von Walddegradierung und Lebensraumwandel auf die Struktur der Vegetation und die Funktionen des Waldökosystems in Borneo. Um die Folgen der Walddegradierung zu verstehen, untersuchen wir Urwald, moderat genutzten Wald und stark genutzten Wald sowie eine Palmölplantage in die zwischen 2000 und 2006 bepflanzt wurde.

Im ersten Kapitel beleuchten wir Forschungsansätze zur Walddegradierung und dem Wandel des Lebensraums im tropischen Regenwald. Viele Studien zeigen nicht nur die Bedrohung tropischer Waldökosysteme, sondern auch Möglichkeiten die Biodiversität von degradierten Wäldern und landwirtschaftlichen Flächen zu verbessern. Die Komplexität der Biodiversität und die Konkurrenz verschiedener Landnutzungsarten haben weltweit einige Biodiversitätsexperimente angeregt. Tatsächlich kann nachhaltiges Wirtschaften und umfassend geplante Holzgewinnung den Biodiversitätsverlust deutlich verringern. In landwirtschaftlich geprägten Landschaften kann die Schaffung von Waldhabitaten innerhalb der landwirtschaftlichen Fläche die Biodiversität und die Ökosystemfunktionen verbessern.

Im zweiten Kapitel messen wir die Baumdichte, die Grundfläche, das Volumen des Totholzes und den gesamten oberirdischen Kohlenstoffbestand in Urwald und degradiertem Wald mit grosser und moderater Holzgewinnung sowie in Palmölplantagen. Unsere Ergebnisse zeigen, dass Walddegradierung die Waldstruktur ändert und den Kohlenstoffbestand verringert. Je intensiver die Holznutzung war, desto geringer waren

die gemessenen Faktoren Baumdichte, Grundfläche, Totholzvolumen und Kohlenstoffbestand. Wir fanden eine positive Korrelation zwischen Kohlenstoffbestand und Grundfläche in allen Waldtypen. Aufgrund der geringeren Kohlenstoffdichte der Ölpalmen, hatten jedoch Palmölplantagen bei gleicher Grundfläche einen deutlich niedrigeren Kohlenstoffbestand. Unsere Ergebnisse zeigen, dass Walddegradierung und Lebensraumwandel die Gliederung der Vegetation verringern und den oberirdischen Kohlenstoffbestand reduzieren.

Im dritten Kapitel untersuchen wir den Einfluss von Walddegradierung und Lebensraumwandel auf jährliche Laubmengen und den Kohlenstoff (C) und Stickstoffgehalt (N) sowie das C:N Verhältnis. Da die Laubmenge von Standort zu Standort variiert, konnten wir keine Unterschiede zwischen den Waldtypen feststellen. Allerdings hatten die Palmölplantagen eine geringere Laubproduktion. Im Vergleich zum Laub der verschiedenen Waldtypen, hatten Ölpalmenblätter den kleinsten C und den höchsten N Gehalt und damit das kleinste C:N Verhältnis. Diese Ergebnisse deuten an, dass Walddegradierung keinen messbaren Einfluss auf die Laubproduktion oder die C und N Konzentrationen hat, wohingegen die Schaffung von Palmölplantagen die Vegetation und ihre Eigenschaften stark verändert.

Im vierten Kapitel untersuchen wir den Einfluss der Walddegradierung auf den Kronenschluss und die Dynamik von Sämlingen in den verschiedenen Waldtypen. An den untersuchten Standorten fanden wir Sämlinge aus 63 Pflanzenfamilien, wobei Fabaceae, Euphorbiaceae und Annonaceae Arten in den meisten Waldtypen vertreten waren. In unbewirtschaftetem Wald ist der Kronenschluss dichter als bei moderater oder starker

Holznutzung. Während Weine und krautige Pflanzen in stark genutztem Wald häufiger sind, gibt es dort weniger Sämlinge. Der Basisdurchmesser der Sämlinge unterschied sich nicht signifikant zwischen den Waldtypen. Die Analyse der Varianzkomponenten deutet an, dass die Pflanzenart die natürliche Regeneration durch Sämlinge beeinflusst.

Im fünften Kapitel diskutieren wir zusammenfassend die Ergebnisse der Kapitel zwei, drei und vier. Wir stellen Ideen für zukünftige Forschungsprojekte vor um Wissenslücken im Bereich der Degradierung von tropischen Wäldern und dem Lebensraumwandel zu schliessen. Zudem schlagen wir mehrere Bewirtschaftungsmethoden für degradierten Wald und Palmölplantagen vor, die die Biodiversität verbessern können. Durch die Beschreibung der ursprünglichen Bedingungen vor der Fragmentierung tragen die Ergebnisse dieser Arbeit einen wichtigen Teil zum SAFE Projekt bei. All dies ist unerlässlich zur Unterstützung der Bemühungen zur Wahrung der Biodiversität in degradierten Wäldern und zum Verständnis der Auswirkungen von Lebensraumwandel in den tropischen Regenwäldern Südostasiens.

CHAPTER 1

General Introduction

Research rationale of tropical forest habitat change

Tropical forests are complex ecosystems recognized as one of the most productive and species rich natural communities in the world (Gardner et al., 2010; Putz et al., 2001). Many reviews, experiments and models have quantified the relationship between biodiversity and ecosystem functioning at local, regional and global scales (Cardinale et al., 2009; Hector and Bagchi, 2007; Isbell et al., 2011; Koh and Sodhi, 2010). Human activities, such as timber extraction and agricultural expansion, have however caused changes within tropical forests landscapes (Benhin, 2006; DeFries et al., 2005; Rist et al., 2011; Riswan and Hartanti, 1995). The consequences of such activities are large losses of original old growth forests, the creation of large areas of degraded forests, a decrease in forest habitat area and the decline of biodiversity within tropical forests (Achard et al., 2002; Wilcove et al., 2013). Understanding the impact of changes in forest habitats on natural ecosystems will require the integrated management of different elements within the landscape. In this study, we therefore examine the effects of forest degradation and forest habitat change as a result of oil palm plantation on ecosystem functioning.

Deforestation of tropical forest

Degraded forest area has increased as a result of forest exploitation and agricultural development. Both activities contribute to the acceleration of the rate at which forest habitats changes and the consequent effects on local and global climate, local landscapes, species extinctions, and carbon emission in tropical forests worldwide. The changes observed in forest structure and composition after years of logging may contribute to changes in the functioning of these ecosystems. Degraded forests frequently exhibit changes in ecosystem functioning, a stressed wildlife community and contain damaged remnant vegetation. Forest degradation and changes in forest habitat have resulted in a great loss of biodiversity as old growth forest ecosystems are among the most species rich. Previous studies have demonstrated that forest ecosystem are a carbon sink, and deforestation therefore results in the releases carbon into the atmosphere (Malhi and Grace, 2000; Phillips, 1998; Phillips and Lewis, 2013). This knowledge has broadened the research perspective of forest biodiversity conservation, specifically the impacts of forest degradation and deforestation. Indeed, long-term observations are required to understand the recovery of biodiversity following forest degradation and deforestation, particularly in the context of improved species richness through succession processes (Sodhi et al., 2010).

Deforestation of global tropical forests between 1990 and 1997 caused an annual loss of 5.8 million hectares in addition to the visible degradation of 2.3 million hectares of forest (Achard et al., 2002). Miettinen et al. (2011) found that between year 2000 and 2010 deforestation of forest cover in Southeast Asian declined 1% annually. Giree et al. (2013) and Hansen et al. (2009) used remote sensing data to monitor forest cover in Malaysia and Indonesia, respectively. They found annual losses of forest area in both countries were among the highest in the Southeast Asia region. The decline in forest cover threatens numerous forest species and may contribute to an increase in carbon dioxide concentration in the atmosphere.

An assessment by the Food and Agriculture Organisation (FAO) indicated that worldwide afforestation and restoration occurred. These activities have helped to increase forest areas in regions where degraded land and forests are otherwise being replaced by plantations of fast growing timber and pulpwood (FAO, 2010). The report stated that net change in global forest area from year of 2000 to 2010 was estimated at 5.2 million hectares annually, down from an annual 8.3 million hectares from 1990 to 2000.

In terms of logging, over-exploitation of timber through harvesting has resulted in damage to forest structure, changes in species composition and a decrease in the density of remnant trees. Forests that are frequently or heavily logged have been classified as unproductive and uneconomical areas, and it is highly probable that such areas will be converted to agriculture. The expansion of agriculture has led to a rapid increase in the logging of forests resulting an increase of deforestation rate in Southeast Asia (Miettinen et al., 2011). Malik et al. (2013) reported that forests in Malaysia were managed in a sustainable manner for economic reasons, ecological balance and environment stability, which successfully maintained forest areas at 59% of total land area. However, Giree et al. (2013) found that expansion of oil palm (*Elaeis guinensis*) in Malaysia has been a major cause of deforestation and accelerated the loss of forest habitat. They found an annual loss in gross forest cover in Malaysia of 0.43 million hectare per year during 1990 to 2000 increased to 0.64 million hectare annually during 2000 to 2005.

An increase in the use of palm oil products may therefore potentially lead to a rapid conversion of forests to palm oil plantations accelerating the destruction of tropical forest habitats and the consequent increase in the negative effects on ecosystem functioning and biodiversity globally. To support biodiversity conservation therefore degraded forests have received much attention in an attempt to understand the relationship between ecosystem functioning and biodiversity richness (Hector et al., 2011; Naeem et al., 2009). To study the effects of forest degradation and biodiversity change, experiments in modified landscapes from old growth forest to degraded forest and consequent changes in forest habitat have been developed in forests in the Amazon (Laurance et al., 2002) and Borneo (Ewers et al., 2011). These experiments have been used to assess the relationship between forest degradation levels through disturbance intensity and size of forest fragmentation to habitat change. The research findings can be integrated into management strategies for forest conservation and agriculture land use planning.

Tropical forest habitat change

Human activities such as logging and agricultural expansion are the main cause for changes in forest habitat. The conversion of forest habitat to agriculture causes the destruction of natural habitat for some species, which are unable to adapt to the new habitat therefore destroying the community previously found in the natural habitat. These cultivated areas induce alterations at local scales with a substantial negative impact on forest landscapes and the natural ecosystem. The change in forest habitat are not restricted to the loss of biodiversity but may lead to the introduction of invasive species (Wright, 2005), cause an increase in greenhouse gas emissions (Danielsen et al., 2009) and compound local and global climate change (Malhi et al., 2002).

Whereas agricultural expansion leads to the decline of forest habitat, research on forest ecology and biodiversity conservation serves to prevent forest degradation and promotes forest conservation. This competition between forest habitat conservation and agricultural land-use has been heavily debated specifically in terms of global biodiversity conservation.

Indeed, the complexity of forest habitats has spurred the establishment worldwide of forest habitat and fragmentation experiments (Debinski and Holt, 2000). As an example, the Biological Dynamics of Forest Fragments Project (BDFFP) in Amazon forest of Brazil (Laurance et al., 2002); Calling Lake Fragmentation Experiment in Alberta, Canada (Schmiegelow et al., 1997); Wog Wog Habitat Fragmentation in New South Wales, Australia (Margules, 2009) and Stability of Altered Forest Ecosystem (SAFE) project in Sabah, Malaysia (Ewers et al., 2011). These large-scale habitat fragmentation experiments integrate human activity and natural ecosystem response, contributing to our knowledge on how to deal with land-use conflict between agricultural expansion and the conservation of forest habitats.

Ongoing conversion of forests to agricultural land has attracted researchers to conduct studies on the possible integrating forest habitat into agricultural areas (Gardner et al., 2009; Gray et al., 2014; Koh et al., 2009; Luskin and Potts, 2011). Such integration may be important for both biodiversity conservation and ecosystem functioning in agricultural landscapes. Indeed, sustainable land-use management is required to conserve biodiversity and ecosystem services in mixed landscapes (Garnett et al., 2013)

The SAFE Project Experiment

The SAFE project experiment based in Sabah, Malaysia Borneo (Figure 1) located at the South-West of Sabah (4^{o} 38’ N to 4^{o} 46’ N, 116^{o} 57’ to 117^{o} 42’ E). Ewers et al. (2011) elaborated details on the SAFE project site, experiment and sampling design. Reynolds et al., (2011) reviewed land use and forest management in Sabah between 1990 to 2010.

The SAFE project experiment is an area of 7,200 ha, consisting of a mixture of twice-logged lowland dipterocarp forest and oil palm plantations. The forest areas were logged during the 1970s and again from the late 1990s to the early 2000s. The oil palm plantation, planted between year of 2000 and 2006, and in the vicinity of logged forest. The logged forest experimental site allocated for the SAFE Project experimental is within an area that was legally approved for oil palm plantations. The forest fragments, of different species composition will be located in between the planted oil palms. This project will play a major role in establishing initial conditions of pre-fragmentation allowing a better assessment of the impacts of conversion of forests into oil palm plantation.

Conclusion

In this thesis, we examine the effects of forest degradation and habitat change on ecosystem functioning. We sample sites of old growth forest, moderately logged forest, heavily logged forest and oil palm plantation to investigate the variation in the biophysical characteristics between each site. We use the biophysical data of each site to study the effects of forest degradation and habitat change using established allometry equations. We study seedling dynamics, aboveground carbon stocks, litterfall production and leaf litter carbon and nitrogen concentration across forest sites to examine the effects of the conversion of forest habitat change to oil palm plantations. Finally, we discuss the effects of forest degradation and habitat change on ecosystem functioning and how such research may be used to increase the stability of altered forest ecosystems.

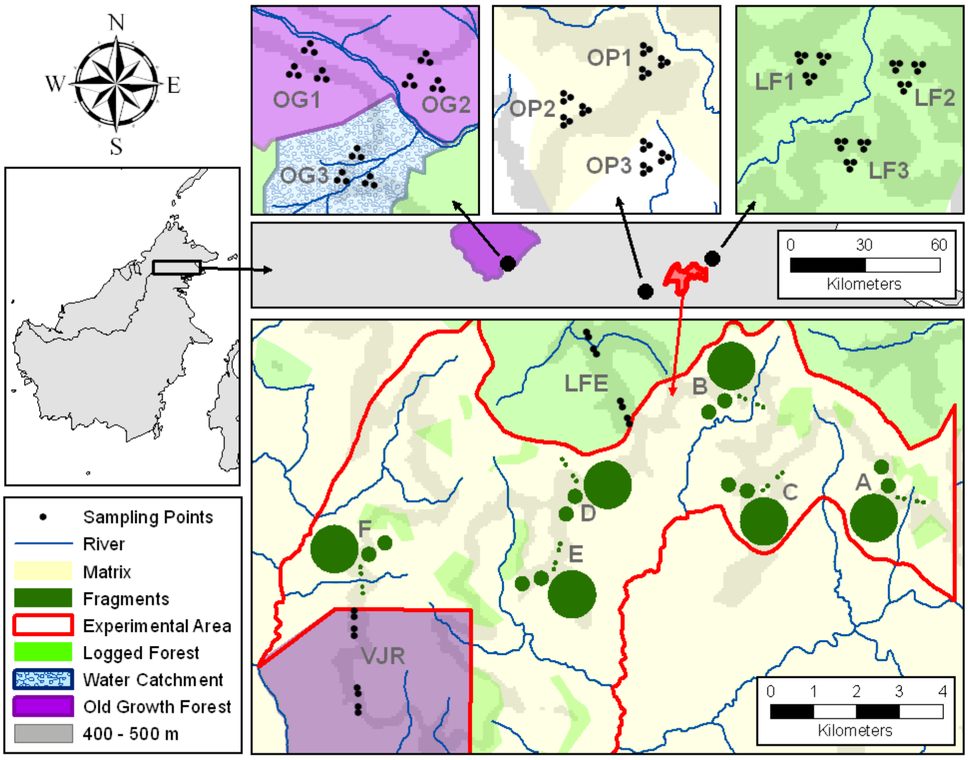

Figure 1: Location map of SAFE Project study area (Ewers et al., 2011). A block of OG1, OG2 is located in primary forest reserve of Maliau Basin Conservation Area (MBCA) and OG3 in water catchment area. Blocks OG1 and OG2 had pristine and never been logged, whereas blocks OG3 slightly logged once with very low disturbance. The SAFE Project experiment is about 70 km distance from the MBCA and nearby with blocks of virgin jungle reserve (VJR), logged forest (LF), logged forest edge (LFE) and oil palm plantation (OP). The VJR was logged once with low disturbance. LF and LFE was logged twice with a selective logging method where timber extracted is subject to demand and the forest stands were intermediately disturbed. OP is the area planted with monoculture of oil palm (*Elaeis guineensis*). The SAFE Project experiment area consists of six blocks of A, B, C, D, E, and F. This area is remnant logged forests were twice logged and the second logging rotation implementing the modified selective system.

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CHAPTER 2

Effects of Forest Degradation and Habitat Change on Vegetation Structure and Carbon Stocks in Bornean Forest

Abstract

We investigated the effects of forest degradation and land use change on vegetation and carbon stocks in the SAFE Project experiment area. We quantified tree density, basal area, coarse woody debris (CWD) volumes and total aboveground carbon (TAGC) stocks in old growth forest and degraded forests that had been moderately logged and heavily logged, as well as in oil palm plantation. We used measurements of diameter breast height and allometric equations to investigate the impacts of forest degradation and habitat change to oil palm on vegetation structure changes and carbon stocks. We combined trees and coarse woody debris to present TAGC stocks across forest types and oil palm plantation. We found forest degradation has affected the forest structure and decreased TAGC stocks. Tree density, basal area, CWD volumes and TAGC stocks decreased with increased logging intensity. A positive correlation between TAGC stocks and basal area was observed across forest types. The TAGC stocks in old growth forest was 132.72 Mg C ha^{-1} (95% CI: 84.68 - 208.46), 70.91 Mg C ha^{-1} (44.60 - 113.12) in moderately logged forest and 46.36 Mg C ha^{-1} (32.72 - 64.87) in heavily logged forest and 10.85 Mg C ha^{-1} (5.93 - 19.92) in oil palm plantation. The reduction of TAGC stocks relative to old growth forest in moderately logged forest was 53%, 65% in heavily logged forest and 92% in oil palm plantation.

Introduction

Deforestation of tropical forest through logging and agricultural development has played an important role in reduction of global carbon stocks (Harris et al., 2012). This rapid land use change (Lugo and Brown, 1992), has influenced the carbon cycle and greenhouse gas emissions(Carlson et al., 2012; Gullison et al., 2007). Deforestation had contributed about 6 - 17% of total anthropogenic carbon emissions (Van der Werf et al., 2009). Harris et al. (2012) reported that global carbon monitoring between 2000 and 2005 has estimated a total tropical forest sink worldwide of 0.8 Pg C year^{-1}, which are correlated with forest cover loss. Latin America and the Caribbean region had the highest forest cover loss, followed by South and Southeast Asia and Sub-Saharan Africa. Global forest loss was estimated at about 2.3 million square kilometers and increased by 0.8 million square kilometers from 2000 to 2012 (Hansen et al., 2013). A recent report by Koh et al. (2013) stated that between 1999 and 2009, the Southeast Asian tropical forest had decreased due to the expansion of oil palm plantation, which caused deforestation rates of 470,000 hectare per year. Achard et al. (2002) and Laurance (2007) reported that Southeast Asia has recorded the highest rates of deforestation among tropical regions.

The exploitation of forest for high value timber has changed forest cover in Southeast Asia. This has created more scattered logged and degraded forest landscape and become common. Unfortunately, degraded forest often subsequently been converted to agricultural causing further rapid loss of forest habitat and biodiversity (Sodhi et al., 2004). However, degraded forest areas were identified as important for forest communities of various taxa, including insects, plants and animals. In recent years, degraded forests were widely studied to evaluate and understand their characteristics (Berry et al., 2010; Chazdon et al., 2009; Edwards et al., 2011; Fisher et al., 2011; Gibson et al., 2011).

Logging activities have damaged the forest structure, produced lower tree density and less of basal area, and low canopy density (Imai et al., 2012; Okuda et al., 2003; Saner et al., 2012). These widespread changes have caused a reduction in timber yield of 46% after first harvest. However 76% of carbon is still retained in once-logged forest and 85-100% of species of mammals, birds, invertebrates, and plants remain after logging (Putz et al., 2012). Many studies on the biomass and aboveground carbon stocks in Borneo forest indicated that logging have affected the forest composition, altering the biomass and aboveground carbon stocks in different forest types (Morel et al., 2011; Pinard and Putz, 1996; Saner et al., 2012; Singh et al., 2014; Tangki and Chappell, 2008).

Other studies have estimated that forest vegetation carbon contains between 47.4% (Martin and Thomas, 2011) and 50% of dry biomass (Brown, 1997). A release of vegetation carbon occurs when these trees die and become coarse woody debris (CWD), which subsequently decomposes. CWD contributes to the aboveground carbon stocks and carbon release back to the atmosphere as carbon dioxide during the decomposition processes (Wang et al., 2010). CWD refers to the woody material that is comprised of fallen and hanging trunks and branches, standing dead trees and stumps (Harmon et al., 1986). Estimates of CWD stocks in tropical forests range from 0 – 60 Mg ha^{-1} and can contain up to 33% of the biomass contained within of trees ≥ 10 cm diameter (Baker et al., 2007). CWD contributes to long-term carbon storage at the global and regional scale (Harmon and Hua, 1991). If it remains on the forest floor and is slow decaying, CWD has the ability to reduce carbon dioxide release

(Brown et al., 1992). CWD is also a source of organic matter and nutrients to the forest soil during decomposition as well as a carbon pool (Clark et al., 2002; Spetich et al., 1999). Logging has removed a large amount of CWD from woody residues and the forest floor layer (Jurgensen et al., 1997). Studies have linked the volume of CWD stocks to forest structure and age (Kissing and Powers, 2010), site topography gradient (Clark et al., 2002; Gale, 2000) and land use change, history and management (Kauffman et al., 2009).

There are still substantial gaps in our knowledge about how CWD and Carbon stocks change between old growth forest, degraded forest and oil palm plantation. We believe that it is crucial to understand how the forest structure, CWD and total aboveground carbon (TAGC) stocks are affected by logging intensity, and conversion of forest to oil palm. In this study, we evaluated the effects of forest degradation on vegetation structure, TAGC stocks of trees above 10 cm diameter breast height, CWD volumes and carbon stocks above 10 cm diameter. To assess the effect of forest degradation and habitat change, we classified the sampling sites into three forest types: old growth forest, moderately logged forest and heavily logged forest, and oil palm plantation. We asked the following questions: (1) Does the forest degradation gradient influence forest structure? (2) Does CWD volume and CWD carbon stocks differ between sites? (3) Does forest habitat change reduce TAGC stocks? The associated objectives were (1) to determine the current forest structure after different logging intensities, (2) to investigate whether forest degradation and habitat change can influence the abundance of CWD and (3) to compare TAGC in old growth forest, logged forest and oil palm plantation.

Methods

Study area

This study is part of the Stability of Altered Forest Ecosystems (SAFE) Project experiment, which is located in the South-West of Sabah, Borneo, Malaysia (4^o 38' N to 4^o 46' N, 116^o 57' to 117^o 42' E). The SAFE Project area consists of mixed landscapes of oil palm plantation, logged forest and unlogged forest (in the Maliau Basin Conservation Area) (Figure 1). The SAFE project experiment is a large initiative designed to understand the ecological impacts of tropical forest habitat change through monitoring of different sizes of forest fragments (Ewers et al., 2011).

Four sites were sampled: old growth forest, moderately logged forest, heavily logged forest, and oil palm plantation. Old growth forest ranged from undisturbed to very low disturbance, where two forest stands in blocks OG1 and OG2 were pristine and had never been logged, whereas stands in blocks OG3 and VJR were lightly logged once. Moderately logged forest (blocks LF1, LF2, LF3 and LFE) was logged twice with a selective logging method, where timber extraction is subject to demand. Heavily logged forest (blocks A, B, C, D, E, and F) are in logged forests that twice logged with the second logging rotation implementing the modified selective system. Both moderately logged and heavily logged forests were logged once during the 1970s and a second time from the late 1990s to the early 2000s. The heavily logged forest had high density of logging roads, timber stumping areas and skid trails, with only a few commercial and emergent trees remaining and the rest of the community dominated by pioneer tree species. As part of the larger SAFE experiment, the heavily logged forest area is in the process of being fragmented. During this process, blocks A, B, C, D, E and F will become forest fragments and the rest of the landscape is oil palm plantation. Oil palm plantation (blocks OP1, OP2 and OP3) is an area planted with a monoculture of oil palm (*Elaeis guineensis*) of between four and ten years old. For a detail description of sampling, see Table 1.

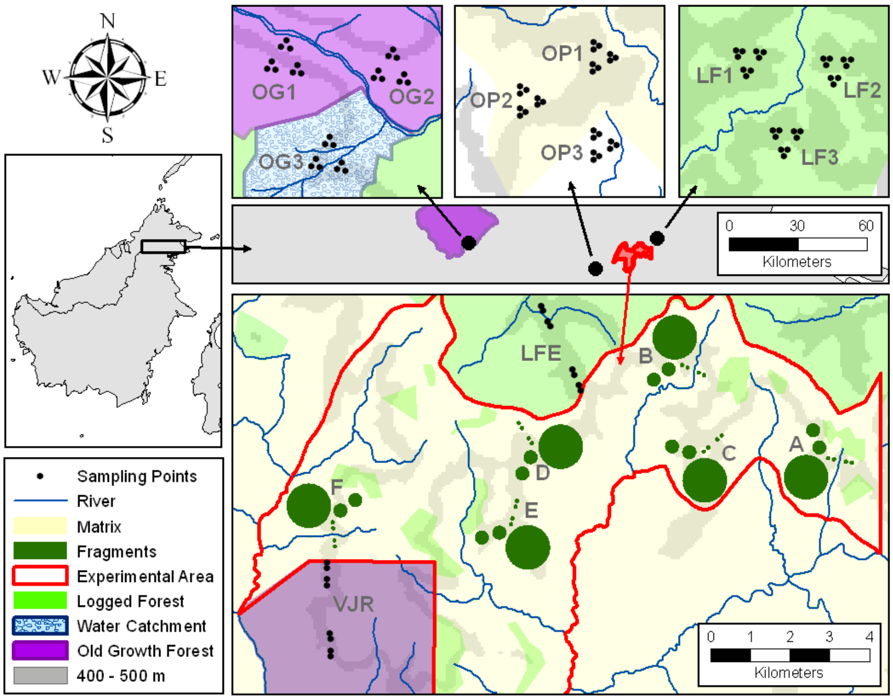

Figure 1: Location map of SAFE Project study area (Ewers et al., 2011).

Table 1: Descriptions of samplings across the study area

Site	Logging intensity	Logging history	Block	Forest quality (range)*	Number of sampling	Total sampling sizes (Hectare)
Old growth forest	Undisturbed	Never	OG1	4.44 (3-5)	9	0.56
	Undisturbed	Never	OG2	4.88 (4-5)	9	0.56
	Very low	Low intensity	OG3	4.22 (3-5)	9	0.56
	Low	Variable	VJR	3.43 (2-5)	8	0.50
Moderately logged forest	Intermediate	Twice	LF1	3.22 (3-4)	9	0.56
	Intermediate	Twice	LF2	3.67 (3-4)	9	0.56
	Intermediate	Twice	LF3	3.44 (3-4)	9	0.56
	Intermediate	Twice	LFE	3.25 (2-4)	8	0.50
Heavily logged forest	High	Twice	A	2.25 (1-4)	16	1.00
	High	Twice	B	2.75 (2-4)	16	1.00
	High	Twice	C	2.06 (1-4)	16	1.00
	High	Twice	D	2.06 (1-3)	16	1.00
	High	Twice	E	1.94 (1-4)	16	1.00
	High	Twice	F	2.50 (1-3)	16	1.00
Oil palm plantation	NA	Cleared	OP1	N.A.	9	0.56
		Cleared	OP2	N.A.	9	0.56
		Cleared	OP3	N.A.	9	0.56

*Forest quality range is a score on qualitative scale of 1 - 5, (1) very poor, no standing trees, open canopy with ginger, vines or low scrub, (2) poor, open canopy with occasional small trees over a ginger and vine layer; (3) okay, small trees abundant and canopy at least partly closed; (4) good, lots of trees including some large trees and a closed canopy; (5) very good, no evidence of logging, closed canopy with large trees (Ewers et al., 2011).

Data collection

Forest inventory data of 193 vegetation plots from four sites were used to analyze the vegetation structure, tree aboveground carbon stocks and CWD volumes and carbon stocks. The vegetation and CWD were surveyed in 25 m x 25 m of vegetation plots following the RAINFOR protocols (http://www.rainfor.org/en/manuals). All trees above 10 cm at diameter breast height (DBH) were identified, tagged and measurement, and tree height was recorded. The vegetation inventory dataset were used to calculate tree density and basal area of each site.

A CWD census was carried out using a plot-based measurement. CWD, including all branches above 10 cm diameter, were recorded and identified as being fallen, standing, hanging or a stump. The length and both diameter of both ends fallen and hanging CWD were recorded. Measurements of length stopped where the deadwood diameter dropped below 10 cm or where the deadwood stretched beyond the plot boundaries. Standing deadwood was measured in a similar way to the living trees, with DBH being recorded at 1.3 m. For stumps over 1.3 m height, another measurement of diameter was taken at the top of the stump, down to a minimum of 10 cm diameter, and the height to this point was recorded. Where the end diameter could not be measured, an estimated was made.

All pieces of CWD were classified into one of five decomposition classes according to RAINFOR protocols (http://www.rainfor.org/en/manuals): namely Class 1- solid wood, recently fallen; Class 2 - solid wood, no fine branches and bark starting to fall; Class 3 – Non solid wood, in poorer condition; Class 4 – soft rotten wood, where nail can be pushed in easily; and Class 5 – soft rotten wood that collapses when stepped on.

Aboveground tree biomass and carbon estimation

The tree aboveground biomass (AGB) of trees over 10 cm diameter breast height was calculated using the allometric equation Model 3 developed by (Basuki et al., 2009) as:

$$\ln(TAGB) = c + \alpha \ln(DBH) + \beta \ln(WD)$$

where TAGB is in kg tree^{-1}, DBH is in cm, c (-0.744) is the intercept, α (2.188) and β (0.832) are the slope coefficient of the regression for mixed species group and WD is wood density in g cm^{-3}. WD value of 0.60 g cm^{-3} is used after clarification by (Morel et al., 2011).

The oil palm trunk and frond biomass was estimated using equations developed by Corley and Tinker (2003) as:

$$\text{Trunk biomass (kg)} = \pi \text{ x } (r \text{ x } z)^2 \text{ x } 100 \text{ x } h \text{ x } \rho$$

$$\rho = (x \text{ x } 0.0076 + 0.083)/1000$$

$$\text{Frond biomass (kg)} = 0.102 \text{ x } l \text{ x } d + 0.21$$

where r is the radius of the trunk (in cm) without frond bases, ρ is trunk density in kg m^3 dependent on the age, x, in years of the palm. *Z* is the ratio of diameter below frond bases, estimated to be 0.777 and h is the height of trunk (in m) to the base of the fronds. Frond biomass equation counted l as the length of petiole (in cm) and d is the depth of petiole (in cm).

CWD and carbon estimation

The CWD were surveyed based on the plot-based measurement method and volume was estimated using Smalian's formula as:

$$V = L\left[\frac{\pi(D_1/2)^2 + \pi(D_2/2)^2}{2}\right]$$

where L (m) is the length of the piece of CWD, and D is the diameter (m), at both ends. Due the absence of CWD density with increasing level of decomposition, we classified CWD density into one of five decomposition classes according to RAINFOR protocols (http://www.rainfor.org/en/manuals). To estimate the CWD biomass, a mean proportion of solid wood spaces of 0.97 was used to adjust the values from external volume to total the individual CWD volume. This was then multiplied by wood density, following one of five decomposition classes developed for Amazonia forest (Baker et al., 2007). We converted CWD, tree and palm biomass to carbon as assuming this was 50% of the dry mass (Kenzo et al., 2010; Saner et al., 2012).

Analysis

Owing to a skewed distribution, we log-transformed the data prior to analysis. The response variables (tree density, carbon stocks, CWD volume and carbon stocks) were modelled as a function of forest type (n = 4) as the fixed effect, with block included as a random effect (n = 17). We used Linear Mixed-Effects Model (lme) nlme packages from R version 2.15.3 (R Development Core Team 2011) for the analyses (Crawley, 2012; Pinheiro and Bates, 2009). We present the mean estimates with 95% confidence intervals, and TAGC stocks as a function to tree basal area with an interaction between TAGC stocks and habitat change.

Results

Comparison of tree density, basal area and aboveground carbon stocks

Tree density was significantly different between sites (Figure 2a; $F_{3,13} = 14.38$, $P < 0.0002$). Tree density decreased from old growth forest to oil palm plantation, where old growth forest contained 504 trees ha^{-1} (95% CI: 347 - 732), 410 trees ha^{-1} (283 - 597) in moderately logged forest, 257 trees ha^{-1} (200 - 332) in heavily logged forest, and 101 trees ha^{-1} (66 - 156) in oil palm plantation.

The tree basal area was also significantly different between sites (Figure 2b; $F_{3,13}$ = 19.54, $P <$ 0.0001), with oil palm plantation 33.89 m^2 ha^{-1} (95% CI: 22.99 – 49.96) being higher compared to other forest types. Among forest types, basal area in old growth forest was 29.54 m^2 ha^{-1} (95% CI: 21.05 – 41.45), which is higher than moderately logged forest with 15.96 m^2 ha^{-1} (11.37 – 22.39) and 9.12 m^2 ha^{-1} (7.18 – 11.58) in heavily logged forest.

The tree aboveground carbon stocks were significantly different among sites (Figure 2c; $F_{3,13}$ = 51.38, $P <$ 0.0001), Tree aboveground carbon stocks in old growth forest was 114.08 Mg C ha^{-1}; 95% CI: 74.07 – 175.69), which is higher compared to the moderately logged forest with 52.98 Mg C ha^{-1} (34.40 – 81.60), 28.53 Mg C ha^{-1} (20.93 – 38.90) in heavily logged forest and 2.99 Mg C ha^{-1} (1.82 – 4.91) in oil palm plantation.

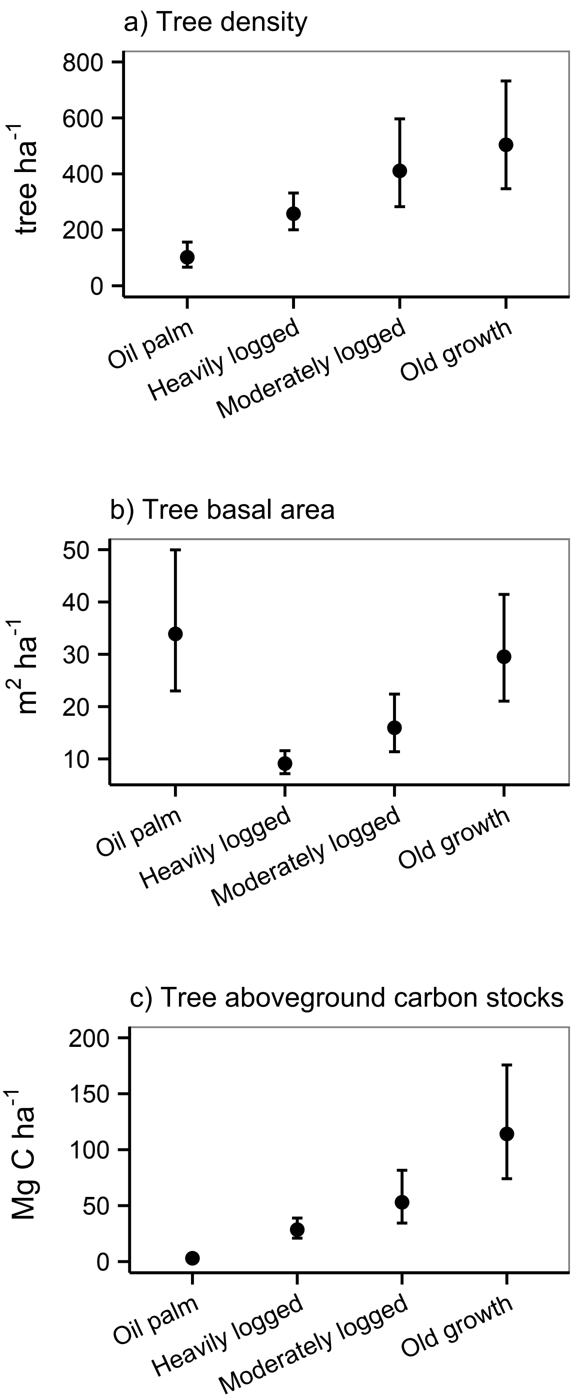

Figure 2: Tree density (a), tree basal area (b) and tree aboveground carbon stocks (c) across sites. Black circles show means with 95% CI.

Comparison of CWD volume stocks

We found that CWD volumes did not differ significantly between sites with the power of this analysis (Figure 3a; $F_{3,13} = 1.78$, $P < 0.19$). We found that CWD volume in old growth forest was 82.32 m^3 ha^{-1} (95% CI: 40.45 – 167.50), in moderately logged forest was 78.96 m^3 ha^{-1} (38.81 – 160.68), in heavily logged forest was 73.03 m^3 ha^{-1} (43.14 – 123.64) and in oil palm plantation was 29.81 m^3 ha^{-1} (13.17 – 67.38). Values of mean CWD in oil palm plantation were never as high as those in the three forest types (range of 73.03 m^3 ha^{-1} to 82.32 m^3 ha^{-1}).

The pattern of CWD volumes according to CWD types indicated that fallen trunks contributed the highest volume across sites (Figure 3b). The CWD volumes of fallen trunks in old growth forest was 60.69 m^3 ha^{-1} (95% CI: 30.22 – 121.89), in heavily logged forest was 52.76 m^3 ha^{-1} (31.68 – 87.87), in moderately logged forest was 48.66 m^3 ha^{-1} (24.23 – 97.73) and in oil palm plantation was 19.87 m^3 ha^{-1} (8.93 – 44.23). Standing deadwood contributed the second highest amount to CWD volumes in old growth forest and moderately logged forest, with 8.88 m^3 ha^{-1} (95% CI: 4.69 – 16.81) in old growth forest and 8.45 m^3 ha^{-1} (4.46 – 15.99) in moderately logged forest (Figure 3c). Meanwhile tree stumps were the second highest contributor and oil palm plantations, with 6.39 m^3 ha^{-1} (95% CI: 3.67 – 11.09) in heavily logged forest and 4.15 m^3 ha^{-1} (1.75 – 9.81) in oil palm plantation (Figure 3d). Hanging branches contributed the lowest amount to CWD volumes in oil palm plantation with only 1.14 m^3 ha^{-1} (95% CI: 0.74 – 1.77), 2.06 m^3 ha^{-1} (1.62 – 2.63) in heavily logged forest and 1.72 m^3 ha^{-1} (1.17 – 2.53) in moderately logged forest (Figure 3e). In contrast, stumps in old growth forest contributed the least to CWD volumes with only 1.28 m^3 ha^{-1} (95% CI: 0.61 – 2.72) (see Figure 3; Appendix 1).

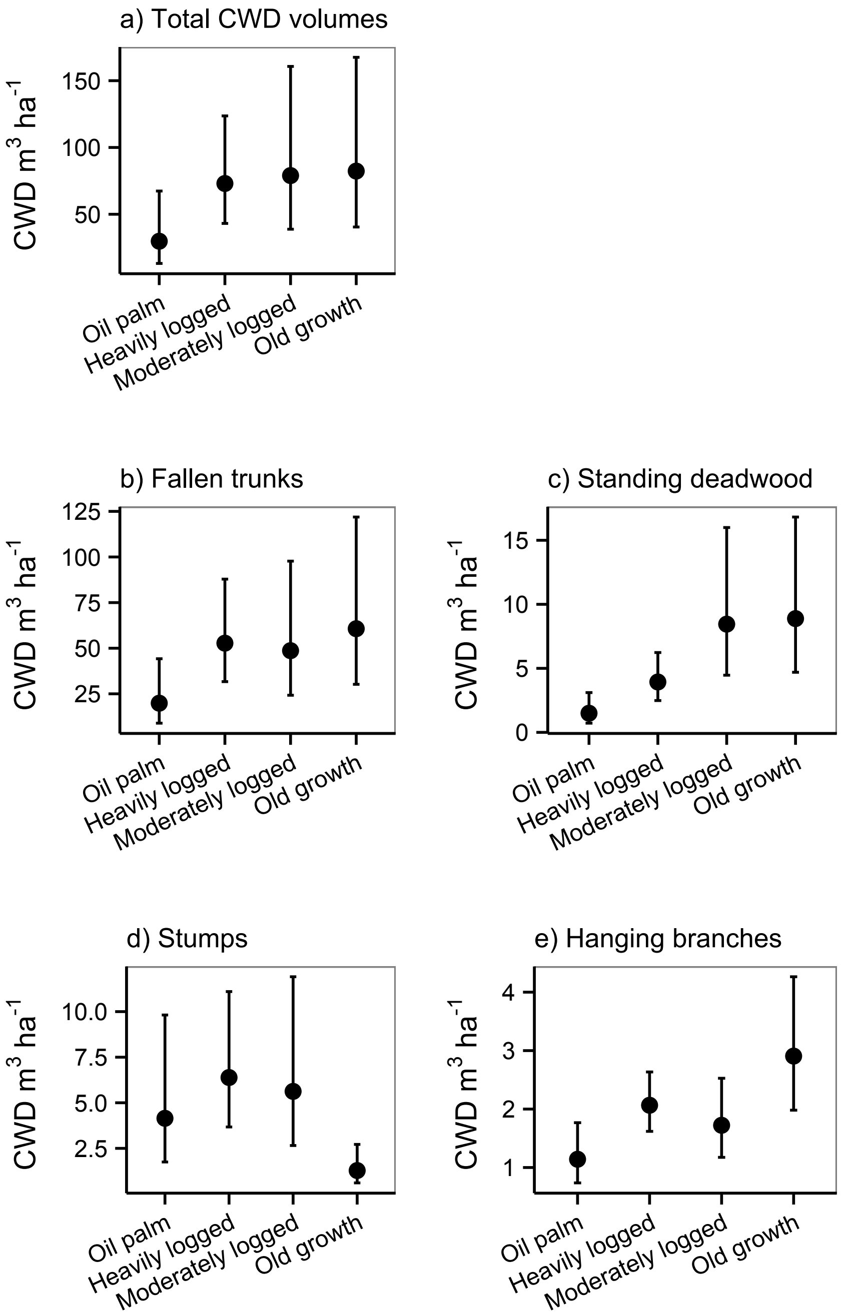

Figure 3: Distribution of total CWD volume and composition of CWD volumes across sites. Black circles represent mean CWD volume and lower and upper bounds 95% CI.

Comparison of carbon stocks

The CWD carbon stocks were not significantly different between sites (Figure 3a; $F_{3,13}$ = 2.15, $P < 0.14$). The CWD carbon stocks in old growth forest were 18.64 Mg C ha^{-1} (95% CI: 10.61 – 32.77), in moderately logged forest were 17.93 Mg C ha^{-1} (10.20 – 31.52), in heavily logged forest were 17.83 Mg C ha^{-1} (11.79 – 26.97) and in oil palm plantation were 7.86 Mg C ha^{-1} (4.11 – 15.01).

A composition of CWD carbon stocks indicated that fallen trunks contributed the highest carbon stocks among sites. The CWD carbon stocks of fallen trunk in old growth forest was 13.91 Mg C ha^{-1} (95% CI: 8.07 – 23.96), in heavily logged forest was 13.07 Mg C ha^{-1} (8.81 – 19.39), in moderately logged forest was 11.18 Mg C ha^{-1} (6.49 – 19.27) and in oil palm plantation was 5.86 Mg C ha^{-1} (3.14 – 10.93). Standing deadwood contributed the second highest amount to CWD carbon stocks in old growth forest (3.21 Mg C ha^{-1}; 95% CI: 2.10 – 4.89) and in moderately logged forest (3.26 Mg C ha^{-1}; 2.14 – 4.97). Meanwhile, stumps contributed the second highest in heavily logged forest (2.73 Mg C ha^{-1}; 95% CI: 1.96 – 3.81) and oil palm plantation (1.97 Mg C ha^{-1}; 1.17 – 3.31). Hanging branches contributed the lowest amount to CWD carbon stocks in oil palm plantation (1.06 Mg C ha^{-1}; 95% CI: 0.82 – 1.37), heavily logged forest (1.39 Mg C ha^{-1}; 1.21 – 1.61) and moderately logged forest (1.23 Mg C ha^{-1}; 0.98 – 1.54). In contrast, the stumps contributed the lowest amount to carbon stocks in old growth forest (1.13 Mg C ha^{-1}; 95% CI: 0.72 – 1.77) (see Figure 4; Appendix I).

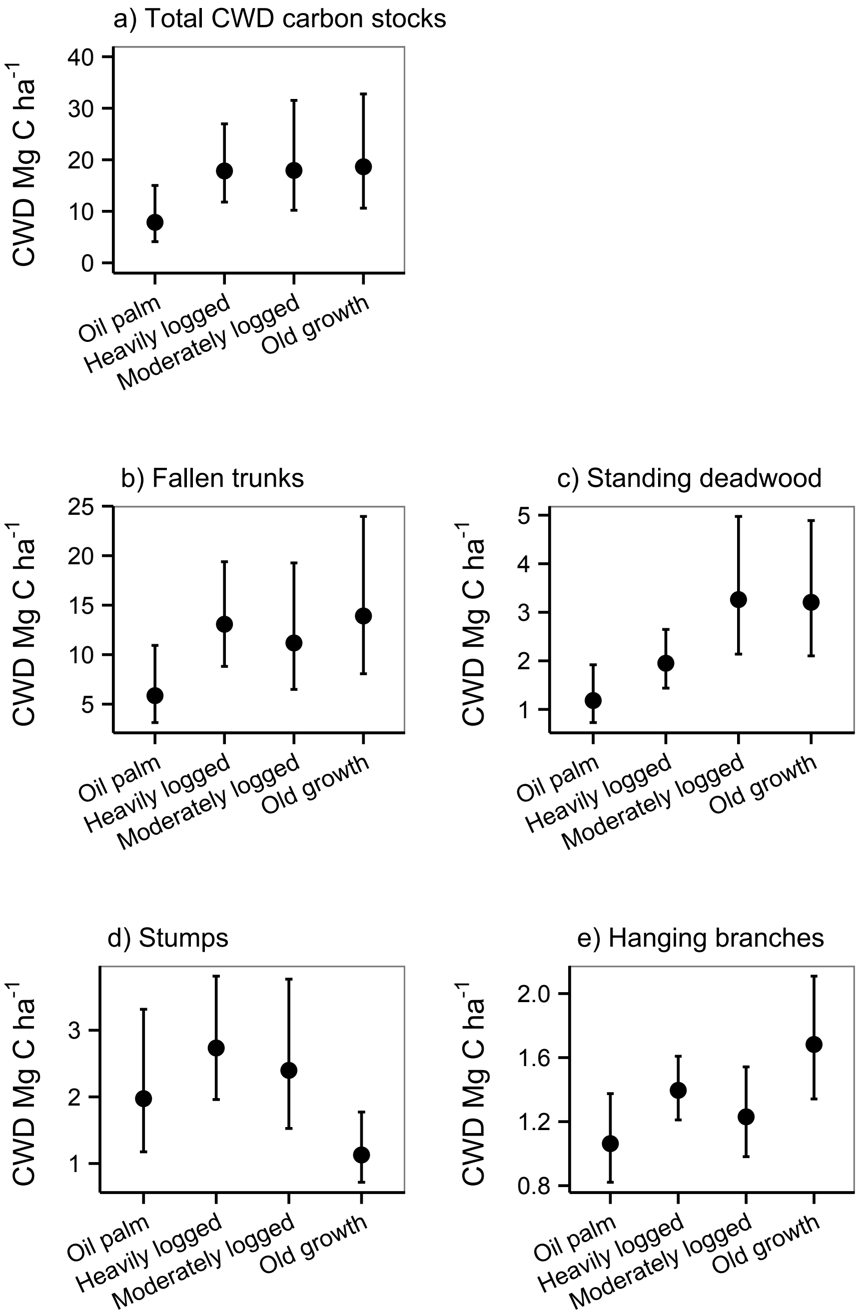

Figure 4: Pattern of CWD carbon stocks and composition across sites. Black circles represent mean CWD carbon stocks and lower and upper bounds 95% CI.

Pattern of TAGC stocks

A positive relationship was found between TAGC stocks and forest types from heavily logged forest to moderately logged forest and then to old growth forest (Figure 5A). CWD carbon stocks showed no clear differences between forest types (Figure 5B). Comparison between sites indicated that oil palm plantation had the higher basal area but contained the lowest TAGC stocks (Figure 5C). We found that TAGC stocks decreased with increasing of forest degradation. TAGC stocks were lowest in oil palm plantation at 10.85 Mg C ha^{-1} (95% CI: 5.93 - 19.92) increasing to 46.36 Mg C ha^{-1} (32.72 - 64.87) in heavily logged forest, 70.91 Mg C ha^{-1} (44.60 - 113.12) in moderately logged forest and 132.72 Mg C ha^{-1} (84.68 - 208.46) in old growth forest. TAGC stocks were 77%, 85% and 92% higher in heavily logged forest, moderately logged forest and old growth forest respectively compared to oil palm plantation. TAGC stocks in old growth forest were greater by about 65% and 47% compared to heavily logged forest and moderately logged forest.

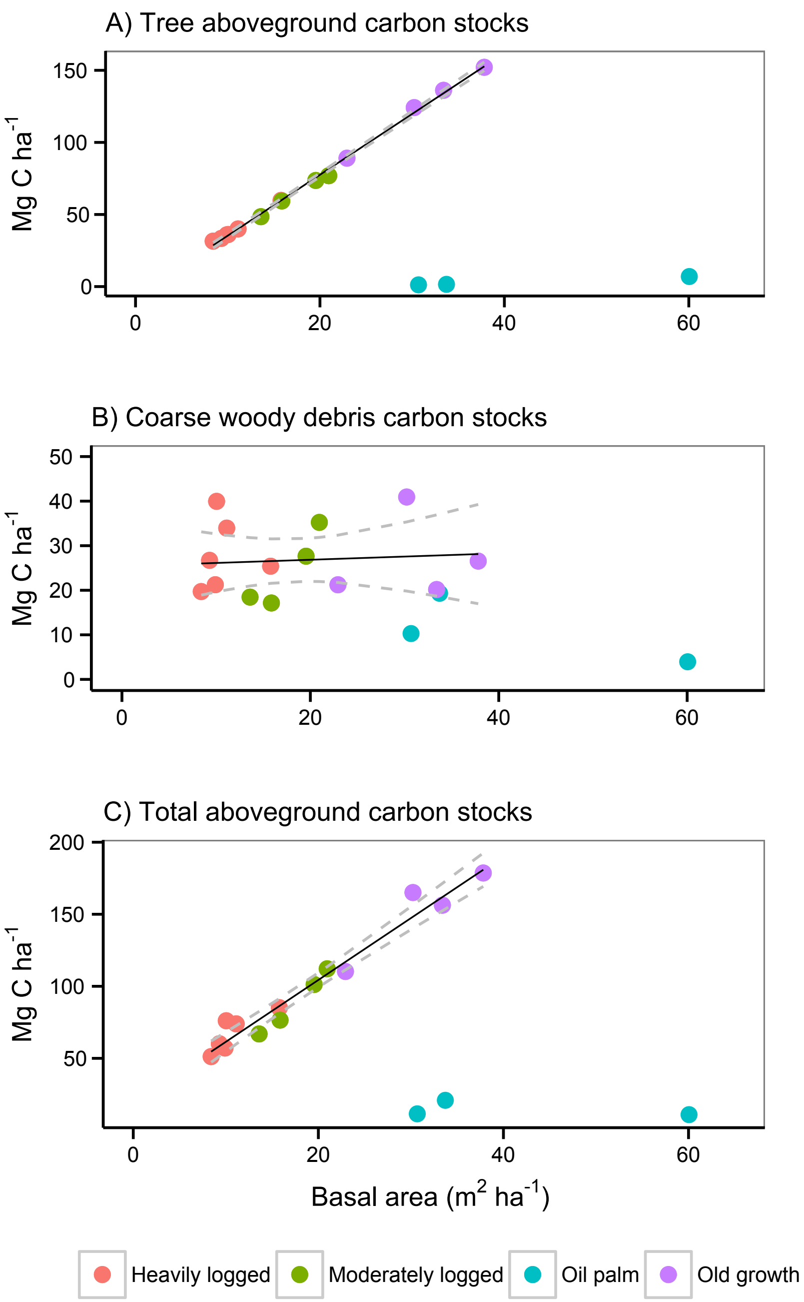

Figure 5: Carbon stocks as a function of tree basal area for (A) tree aboveground carbon stocks (B) CWD carbon stocks and (C) total aboveground carbon stocks. Solid lines represent model prediction and lower and upper bounds 95% CI. Note that while the forests from a continuum the oil palm plantation plots are outliers in almost all cases.

Discussion

The effects of forest degradation and habitat changes on biodiversity conservation and ecosystem function in tropical regions has been the focus of many studies (Gardner et al., 2010; Lewis, 2009; Sodhi et al., 2010). In this investigation, we compared forest structure, CWD and aboveground carbon stocks in old growth forest, moderately logged forest, heavily logged forest and oil palm plantation within the SAFE Project experiment area. We found that forest degradation and habitat conversion to oil palm plantation caused a decrease in tree density, basal area, CWD volumes and TAGC stocks.

Effects of forest degradation and habitat change on vegetation structure.

We found that forest degradation reduced tree density and tree basal area. Obviously, habitat change from forest to oil palm plantation strongly influenced the characteristics of vegetation structure. The level of reduction of tree density and basal area from unlogged forest to logged forest that we observed was similar to other studies elsewhere in Borneo (Tangki and Chappell, 2008; Saner et al., 2012). These can explained by the direct impact of logging (Iskandar et al., 2006; Okuda et al., 2003; Pinard and Putz, 1996; Sist and Nguyen-Thé, 2002). High logging intensity in heavily logged forest results in lower tree density and basal area compared to moderately logged forest. This difference was caused by high logging intensity and extraction of 179 m^3 ha^{-1} volumes of timber in the heavily logged forest site (Struebig et al., 2013).

The difference in vegetation structure between heavily logged forest and moderately logged forest can explain the level of logging intensity, which will lead to more damage to remaining forest. A study comparing reduced impact logging and conventional logging conducted by Pinard and Putz (1996) at the nearby Danum Valley observed that logging technique had a strong impact on the remaining forest trees. They found that forest structure after reduced impact logging with comprehensive guidelines and low logging intensity resulted in a higher tree density compared to conventional logging techniques.

Even so, we found that heavily logged forest still contained about 30% of the tree basal area, produces 25% of the aboveground carbon stock of old growth forest. Heavily logged forest also produced 90% higher tree aboveground carbon stocks compared to oil palm plantation. A study on biomass in forest and oil palm plantation carried out near to our study site by Morel et al. (2011) discovered that the pattern of aboveground biomass in modified landscapes was heavily influenced by the forest type, management and logging history. In this study, oil palm plantation contributed the highest basal area of any land-use type but also has a lower tree density. Our results differ from those of Morel et al. (2011) and there are limited other studies with which to compare our results. A particular difficulty is the impact of oil palm age on carbon stocks, which also differs between studies. However, in general we found similar results to other studies, where forest conversion to oil palm plantation caused significant carbons losses (Table 3).

Effects of forest degradation and habitat change on CWD stock.

We detected no statistical significant difference in volume and carbon stock of CWD across sites, although both were lower in oil palm plantation. Values of CWD in oil palm plantation were never as high as in the three forest types (Figure 3a and Figure 4a). These findings indicate that logged forests still carry out important ecosystem functions, where vegetation communities naturally will recover and adapted to their environment to performing the ecosystem function (Aerts and Honnay, 2011; Edwards et al., 2011). The conversion of forest to oil palm plantation has affected the amount of CWD stocks. We found that removal of trees significantly reduced the CWD volume from 82.32 m^3 ha^{-1} in old growth forest to 29.81 m^3 ha^{-1} in oil palm plantation. The difference of CWD volumes between old growth forest and logged forest was about 4.34% for heavily logged forest and 3.80% for moderately logged forest. This reduction in CWD volume was similar to that discovered by Gale (2000), although the standing CWD volume was much lower.

The composition of CWD stocks in forest types was strongly influenced by intensity of disturbance (Figure 3). We found that fallen trees contributed the most to CWD carbon stock across sites. Surprisingly, CWD carbon stocks were not significantly different between forest types, except compared to the oil palm plantation (Table 2). The CWD carbon stock was reduced from 18.64 Mg C ha^{-1} in old growth forest to 7.86 Mg C ha^{-1} in oil palm plantation, which is about 58% reduction. This study may underestimate the CWD carbon stocks in oil palm plantation, in which the CWD of oil palm fronds after pruning was not calculated.

We also found similar CWD carbon stocks across forest types, with heavily logged forest containing a slightly higher CWD carbon stock compared to moderately logged forest, but still lower than old growth forest. Furthermore, the contribution of fallen trees to CWD was higher in old growth forest (74%) compared to logged forest (62 – 73%). In contrast, the contribution of stumps was higher in logged forest (13 -15 %) compared with old growth forest (5%). The higher contribution of stumps in logged forest reflects the impact of harvesting activities on debris and timber stocks. In contrast, fallen and stump CWD carbon stocks in old growth forest are created by the natural processes of falling or dying mature trees. This finding is in line with a study by Keller et al. (2004), which found that logged forest contained a higher CWD stock compared to undisturbed forest, and that this was mainly caused by harvesting debris and log residue after logging.

We found that CWD carbon stock in logged forest was 18 Mg C ha^{-1} in contrast to 4 Mg C ha^{-1} in Bukit Timah, Singapore as reported by Ngo et al. (2013). The comparison of amount carbon stocks between this study and previous study elsewhere in Southeast Asia was shown in Appendix II. This large difference between studies probably due to the time period after logging, density of logging disturbance, the methodology used and composition classes used for CWD. In this study, the area was logged twice less than 10 years ago. The heavily logged forest was logged twice using a modified selectively logging system, which allows higher timber volumes to be extracted purposely for conversion to agroforestry and agriculture. In contrast, the moderately logged forest was logged twice with a selective logging system, designed for sustainable timber harvesting.

Effects of forest degradation and habitat change on TAGC stocks.

We found that TAGC stocks in forest areas increased with increment of basal area (Figure 5c). This finding was similar to the results of a study conducted by Saner et al. (2012) near Danum Valley. TAGC stocks in this study were lower compared to results reported from other studies (Appendix II). As reported by many studies, the difference in TAGC stocks between sites is likely to reflect the methods and allometry that were used to calculate biomass and composition of CWD. TAGC stocks will also be strongly influences by the location, soil type, topography and gradient of the study sites (Baker et al., 2007; Gale, 2000;

Saner et al., 2012). Furthermore, in this study the TAGC stocks were only calculated for trees above 10 cm dbh and for CWD above 10 cm diameter.

The TAGC resources and stocks in oil palm plantation differed from those in forest. In oil palm plantation, the TAGC stocks are mostly stored in the dry mass of oil palm trunks, fronds and bunches (Aholoukpé et al., 2013). In a review, Aholoukpé et al. (2013) reported that oil palm could increase stored carbon in the soil through recycling oil palm fronds pruning and trunks felled during replanting. Interestingly, this study indicated that even the forest was heavily logged, the TAGC stocks still relatively close to the old growth forest. In contrast, the TAGC stock in oil palm plantation (10.85 Mg C ha^{-1}) is 92% lower compared to old growth forest (132.72 Mg C ha^{-1}), indicating that forest conversion to oil palm plantation results loss of carbon.

However, we did not count the carbon contained in understory vegetation, soil, fine root biomass, leaf litter or pruned oil palm fronds while calculating TAGC. This study should be considered a general estimate of forest and oil palm TAGC stocks. We also did not specify the wood density of all trees and CWD, but instead applied a general dipterocarp wood density (after Morel et al., 2011) and CWD density classes that were developed for Amazonia forest by Baker et al. (2007). Therefore, we suggest a more accurate estimation of TAGC should also take into account all resources of carbon such as understory vegetation, soil, fine root and leaf litter, and also sample the wood density for trees up to species or family identity. In addition, developing a regional CWD wood density by decomposition classes, and accounting for other sources of CWD in oil palm trees such as bunches and pruned fronds, could help improve the estimation of TAGC stocks in both sites of forest and oil palm plantation habitats.

Conclusion

In conclusion, forest degradation and habitat changes had altered vegetation structure and decreased TAGC stocks. We found that forest habitat has maintained a higher CWD and TAGC stocks, but not in oil palm plantation. We showed that the CWD composition of fallen trees, standing deadwood, hanging trunk and branches, and stumps are directly influences by and good indicator of logging intensity. The contribution of CWD into TAGC stocks in old growth forest was 16%, 33% in moderately logged forest, 62% in heavily logged forest and 163% in oil palm plantation. We also found that high logging intensity and forest conversion is likely to have large negative impact on vegetation composition in these habitats. Forest degradation and habitat change alters the vegetation structure and has impact on the ecosystem functioning particularly the TAGC stocks. Therefore, to support the biodiversity and ecosystem functioning in oil palm plantation, we may suggest that: (1) oil palm development should conserve forest areas where possible rather than clearing the entire forest habitat. Remaining trees in these areas will become CWD resources, which may support the amount of TAGC in oil palm landscape; (2) logging operations should implement a sustainable forest management to minimize damage of remaining vegetation. These may maintain and support the ecosystem functioning and persistent biodiversity in degraded forest and oil palm plantation habitats.

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Appendix I

Table of comparison on tree density, basal area, tree carbon stocks and CWD volumes and carbon stocks, and total aboveground carbon (TAGC) stocks between sites (figures represent means and lower and upper bounds of 95% CI).

Components	Estimated mean and lower and upper bounds of 95% CI			
	Oil palm plantation	**Heavily logged forest**	**Moderately logged forest**	**Old growth forest**
Tree density (tree ha^{-1})	101 (66 – 156)	257 (200 – 332)	410 (283 - 597)	504 (347 - 732)
Tree basal area (m^2 ha^{-1})	33.89 (22.99 – 49.96)	9.12 (7.18 – 11.58)	15.96 (11.37 – 22.39)	29.54 (21.05 – 41.45)
Aboveground carbon stocks (Mg C ha^{-1})	2.99 (1.82 – 4.91)	28.53 (20.93 – 38.90)	52.98 (34.40 – 81.60)	114.08 (74.07 – 175.69)
CWD volumes by type (m^3 ha^{-1})				
- Fallen trunks	19.87 (8.93 – 44.23)	52.76 (31.68 – 87.87)	48.66 (24.23 – 97.73)	60.69 (30.22 – 121.89)
- Hanging branches	1.14 (0.74 – 1.77)	2.06 (1.62 – 2.63)	1.72 (1.17 – 2.53)	2.91 (1.98 – 4.26)
- Standing deadwood	1.49 (0.72 – 3.11)	3.94 (2.48 – 6.23)	8.45 (4.46 – 15.99)	8.88 (4.69 – 16.81)
- Stumps	4.15 (1.75 – 9.81)	6.39 (3.67 – 11.09)	5.62 (2.65 – 11.91	1.28 (0.61 – 2.72)
Total CWD volumes (m^3 ha^{-1})	29.81 (13.17 – 67.38)	73.03 (43.14 – 123.64)	78.96 (38.81 – 160.68)	82.32 (40.45 – 167.50)
CWD carbon stocks by type (Mg C ha^{-1})				
- Fallen trunks	5.86 (3.14 – 10.93)	13.07 (8.81 – 19.39)	11.18 (6.49 – 19.27)	13.91 (8.07 – 23.96)
- Hanging branches	1.06 (0.82 – 1.37)	1.39 (1.21 – 1.61)	1.23 (0.98 – 1.54)	1.68 (1.34 – 2.11)
- Standing deadwood	1.18 (0.73 – 1.92)	1.95 (1.44 – 2.65)	3.26 (2.14 – 4.97)	3.21 (2.10 – 4.89)
- Stumps	1.97 (1.17 – 3.31)	2.73 (1.96 – 3.81)	2.40 (1.52 – 3.77)	1.13 (0.72 – 1.77)
Total CWD carbon stocks (Mg C ha^{-1})	7.86 (4.11 – 15.01)	17.83 (11.79 – 26.97)	17.93 (10.20 – 31.52)	18.64 (10.61 – 32.77)
TAGC stocks (Mg C ha^{-1})	10.85 (5.93 - 19.92)	46.36 (32.72 - 64.87)	70.91 (44.60 - 113.12)	132.72 (84.68 - 208.46)

Appendix II

Table showing a list of general comparison on mean trees and CWD carbon stocks (lower and upper bound of 95% CI) across previous studies.

Sites	Carbon Stocks (Mg C ha^{-1})						Reference
	Old growth forest/Unlogged		Logged forest		Oil palm plantation		
	Tree	CWD	Tree	CWD	Tree	CWD	
Ulu segama Forest Reserves, Malua, Sabah, Malaysia	128	n/a	91.9	13.9	n/a	n/a	Saner et al. (2012)
Danum Valley, Sabah, Malaysia	253.2	n/a	85.9	n/a	n/a	n/a	Tangki and Chappell (2008)
Ulu Segama Forest Reserves, Deramakot and Kalabakan region, Sabah, Malaysia	176.5	n/a	55 – 180.5	n/a	1.2 (< 3 yrs old) 26 (4-19 yrs old)	n/a	Morel et al. (2011)
SAFE Project Experiment	114 (74.07 – 175.69)	18.64 (10.61 – 32.77)	28.53 (20.93 – 38.90)[a] 52.98 (34.40 – 81.60)[b]	17.83 (11.79 – 26.97)[a] 17.93 (10.20. – 31.52)[b]	2.99 (1.82 – 4.91) (4-10 yrs old)	7.86 (4.11 – 15.01)	This study
Temengor Forest Reserve, Perak, Malaysia	149	10.8	n/a	n/a	n/a	n/a	DiRocco (2012)
Pasoh area, Negeri Sembilan, Malaysia	201.5	n/a	n/a	n/a	33.9 (27.5 yrs old)		Adachi et al. (2011)
Bukit Timah Nature Reserve, Singapore	167.5	15.6	104.5	4.2	n/a	n/a	Ngo et al. (2013)
Indonesia	254 - 390	n/a	n/a	n/a	n/a	n/a	Murdiyarso and Wasrin (1995)
Surigao del Sur province, island of Mindanao, Philippines	258	n/a	100	n/a	n/a	n/a	Lasco et al. (2006)
Thailand	226.3	n/a	n/a	n/a	n/a	n/a	Adachi et al. (2011)

Note:
n/a: Not applicable
[a] Heavily logged forest
[b] Moderately logged forest

CHAPTER 3

Effects of Forest Degradation and Habitat Change on Litterfall Production and Leaf Litter Carbon and Nitrogen Concentration in Bornean Forest

Abstract

Forest degradation and habitat conversion through timber extraction and agricultural expansion has changed ecosystem services and biodiversity. This situation will almost certainly continue as human populations expand. Understanding the ecosystem processes within degraded forest and agricultural areas are crucial to support biodiversity and ecosystem functioning. These are urgently needed to support sustainable management of degraded forest and agriculture. We evaluated the effects of forest degradation and habitat change on annual litterfall production, and leaf litter carbon (C), and nitrogen (N) concentration and C:N ratio within the SAFE Project experiment area. We sampled litterfall in four sites: old growth forest, moderately logged forest, heavily logged forest and the oil palm plantation. We found litterfall production varied among sites in the range of 1.15 – 8.04 t ha^{-1} y^{-1} but was indistinguishable between forest types although lower in the oil palm plantation. The litterfall production in moderately logged forest was 8.04 t ha^{-1} y^{-1} (95% CI: 6.88 – 9.39 t ha^{-1} y^{-1}), 7.76 t ha^{-1} y^{-1} (6.64 – 9.06) in old growth forest and 6.88 t ha^{-1} y^{-1} (6.23 – 7.62) in heavily logged forest. The litterfall production in oil palm plantation was the lowest with 1.15 t ha^{-1} y^{-1} (95% CI: 0.97 – 1.38). The leaf litter C concentration was very similar among forest types, making up 49.88% (95% CI: 48.21 – 51.60) in old growth forest, 50.21 % (48.53 – 51.95) in moderately logged forest and 50% (95% CI: 48.69 – 51.38) in heavily logged forest. The leaf litter C concentration in oil palm made up only 46.97 % (95% CI: 45.15 – 48.87, lower than the mixed leaf litter in forest habitats. The N concentration was fairly constant between forest types, making up 1.51 % (95% CI: 1.39 – 1.62) in old growth forest, 1.54 % (1.42 – 1.66) in moderately logged forest and 1.66 % (1.57 – 1.76) in heavily logged forest. The leaf litter N concentration in oil palm was 2.16% (95% CI: 1.98 – 2.36), higher that the mixed leaf litter in

forest habitats. The leaf litter C:N ratio differed significantly between forest habitats and oil palm plantation. Oil palm leaves contained a lower C:N ratio compared to the mixed leaves in forest habitats. Forest degradation had little detectable effect on litter quantity and quality. However, conversion to oil palm plantation results in a vegetation with lower litter production but litter much richer in N and with a lower C:N ratio. The leaf litter C:N ratio increased from heavily logged forest was 30.13 C:N ratio (28.45 – 31.90) to 32.72 C:N ratio (30.38 – 35.25) in moderately logged forest and 33.08 C:N ratio (30.71 – 35.63) in old growth forest. Conversion of forest to oil palm plantation reduced litterfall by 83 – 86%, C concentration by 5 – 6%, C:N ratio by 28 – 34% and increased N concentration by 23 – 30%.

Introduction

Litterfall dynamics in degraded forest have been studied widely to understand the natural process of nutrient cycling in tropical ecosystems (Celentano et al., 2010; Saner et al., 2012; Vitousek, 1984). A study by Alvarez-Clare et al. (2013) in a Costa Rican forest found that nutrient dynamics are important for forest productivity. In the context of the forest nutrient cycle, litterfall from aboveground vegetation was important in providing organic matter to the soil surface and contributing to the maintenance of soil fertility (Sayer and Tanner, 2010).

Numerous studies in tropical regions have demonstrated that litterfall production is not obviously influenced by different forest restoration strategies (Celentano et al., 2010), with increasing stand ages (Lugo and Brown, 1992; Ostertag et al., 2008), with varying species richness (Scherer-Lorenzen et al., 2007) or diversity (Wardle et al., 1997). However, soil types and topography does effect vegetation composition and can alter litterfall production and nutrient concentrations, which then influence the decomposition process and nutrient availability (Dent et al., 2006).

Nutrient concentration in leaf litter has been widely investigated in relation to decomposition in different ecosystems (Barlow et al., 2007). Carbon (C), nitrogen (N) concentration and the C:N ratio are generally significant variables in leaf litter studies (Zhang et al., 2008). Differences in C and N concentration in leaf litter is often correlated with litter quality and with decomposition rates (Rogers, 2002). Correlations between mixed-species leaf litter and decomposition have been reviewed by Gartner and Cardon (2004). They found that mass loss for mixed-species leaf litter was 65% higher than for single-species litter.

Although litterfall production and nutrient concentrations in tropical ecosystems have been widely studied, information on litterfall production and leaf litter C and N concentrations for degraded forests and oil palm plantation sites are still limited. To understand and addressed the effects of forest degradation and habitat change, we evaluated litterfall production and leaf litter C and N concentrations across a large-scale of human-modified landscapes in the SAFE Project experiment area. Our specific objectives were to evaluate litter production and leaf litter C and N concentrations and compare then between forest types, from old growth forest to moderately logged forest, heavily logged forest and oil palm plantation. We hypothesized that (1) habitat change affect litterfall production and that it would be similar between forest types, but lower in oil palm plantation; and that (2) leaf litter C:N ratio would decrease from old growth forest to logged forest then to oil palm plantation, due to differences in vegetation structure, composition and canopy density.

Methods

Study area

The study was conducted in the Stability of Altered Forest Ecosystems (SAFE) Project, which is located on the South-West of Sabah Borneo forest, Malaysia (4^{o} 38' N to 4^{o} 46' N, 116^{o} 57' to 117^{o} 42' E). The SAFE Project is based within a 7200 ha area of forest, which is scheduled to be converted to oil palm plantation (Figure 1). The project area consists of unlogged forest, forest with various levels of forest disturbance caused by logging, and oil palm plantation (Ewers et al., 2011).

We sampled litterfall and leaf litter in unlogged forest, moderately logged forest, heavily logged forest and oil palm plantation (Figure 1; Table 1). Unlogged forest ranged from undisturbed to very lightly disturbed (two forest stands in OG1 and OG2 were a pristine and have never been logged, whereas OG3 and VJR were lightly logged once with low disturbance). Moderately logged forest sites (LF1, LF2, LF3 and LFE) was twice logged with a selective logging method, where timber extracted is subject to demand and the forest stands were intermediately disturbed. Heavily logged forest sites (A, B, C, D, E, and F) are in logged forests that were twice logged, with the second logging rotation using a modified selective system. Both moderately logged and heavily logged forests were logged once during the 1970s and a second time from the late 1990s to the early 2000s. The heavily logged forest is schedule to become fragmented during the course of the SAFE Project. It has a high density of logging roads, stumping areas and skid trails, with only a few commercial and emergent trees. It is dominated by pioneer tree species. Oil palm plantation sites (OP1, OP2 and OP3) is the area planted with a monoculture of oil palm (*Elaeis guineensis)* of between four and ten years old.

Experiment design and sampling

Litterfall

The study sites were divided into four habitat sites: old growth forest, moderately logged forest, heavily logged forest and oil palm plantation (Figure 1). At each of the sites, 3 – 6 blocks comprising of 27 - 96 litterfall traps were established (Table 1).

We used 1 m^2 litterfall traps (n = 193) to estimate litterfall production. The traps were installed at 1 meter from the ground and placed at the centre of the SAFE vegetation plots. The litter traps were made from a plastic pipes with wire twisted around their tops to make a rim, and shade netting fixed to this to act as a net for leaf litter. Everything that fell into the trap over approximately 15 days was collected once every six months (n=3). Litter samples were oven dried at 50°C to a constant mass. Dried samples were then separated into leaves, woody material, reproductive parts (fruits, flowers and seeds) and miscellaneous (unidentified items) then weighed separately for biomass.

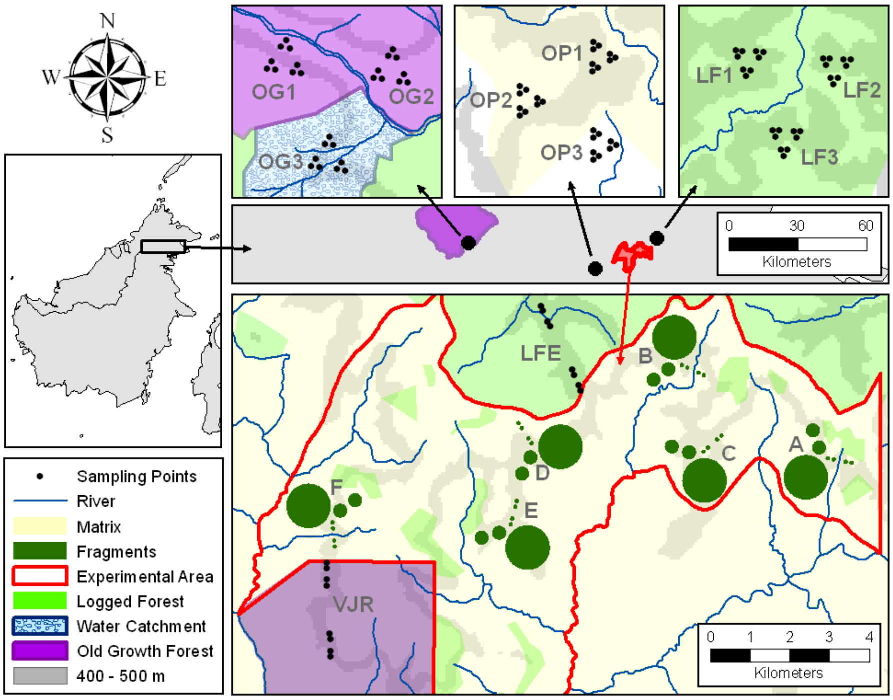

Figure 1: Location map of SAFE Project study area (Ewers et al., 2011).

Table 1: List and description of study site, number of litterfall traps, carbon and nitrogen sampling.

Site	Disturbance level	Logging history	Block	Number of litter traps	Number of C and N samples
Old growth forest	Undisturbed	Never	OG1	9	3
	Undisturbed	Never	OG2	9	3
	Very low	Low intensity	OG3	9	3
	Low	Variable	VJR	8	4
Moderately logged forest	Intermediate	Twice	LF1	9	3
	Intermediate	Twice	LF2	9	3
	Intermediate	Twice	LF3	9	3
	Intermediate	Twice	LFE	8	4
Heavily logged forest	High	Twice	A	16	4
	High	Twice	B	16	4
	High	Twice	C	16	4
	High	Twice	D	16	4
	High	Twice	E	16	4
	High	Twice	F	16	4
Oil palm plantation	NA	Cleared	OP1	9	3
		Cleared	OP2	9	3
		Cleared	OP3	9	3

Leaf litter C and N concentration

The leaf mixtures from litterfall traps were measured for C and N. We used a random technique to choose complete leaves from the second and third litterfall collections across the 193 plots. We pooled two or three litterfall traps for each blocks in the same habitat using a systematic pooling system according to plot numbers to created three or four sampling groups per block (Table 1). We analysed 9 to 24 samples in each habitat type for the C and N concentration. In oil palm plantation, only a small amount of leaf litter was collected in the traps, and most litter on the ground was generating from cut fronds. To sample this, we collected oil palm leaves during the first and second vegetation survey. Several leaves per tree per plot were chosen at random and pooled for analysis.

We pooled 5 – 20 grams of complete leaf litter from each plot according to sampling groups, producing an average of 50 – 60 grams per sample. The samples were oven dried using oven at 60°C to a constant mass, then ground and sieved using a 2 mm mesh to produce leaf litter powder. The C and N concentration in leaf litter powder was then determined with a high temperature combustion process using an Elementar Vario Max C:N analyzer (Elementar Analysensysteme, Hanau, Germany) at the Forest Research Centre, Sepilok, Sabah.

Analysis

Our study focuses on the mean and variability of annual litterfall production and litter C and N concentrations across habitat types. We present a mean estimates with 95% confidence intervals (CI). We used the Linear Mixed-Effect Models (lme) nlme packages from R version 2.15.3 (R Development Core Team 2011) to model the effect of habitat on litterfall characteristics (Crawley, 2012; Pinheiro and Bates, 2009). We log-transformed all data as owing to a skewed distribution. Response variables (litterfall mass, leaf litter C and N concentration and C:N ratio) we modelled against habitat type (n = 4) as a fixed effect and block (n = 17) as a random effect.

Results

Litterfall production

The total litterfall production varied among sites in the range of 1.15 – 8.04 t ha^{-1} y^{-1}. Total litterfall production was significantly different between habitat types (Figure 2a: $F_{3,13}$ = 144.88, P < 0.0001). Total litterfall production was the lowest as1.15 t ha^{-1} y^{-1} (95% CI: 0.97 – 1.38) in oil palm plantation, 6.88 t ha^{-1} y^{-1} (6.23 – 7.62) in heavily logged forest and 7.76 t

ha^{-1} y^{-1} (95% CI: 6.64 – 9.06) in old growth forest. Moderately logged forest has the highest litterfall by 8.04 t ha^{-1} y^{-1} (95% CI: 6.88 – 9.39), and was 3%, 14% and 86% higher than in old growth forest, heavily logged forest and oil palm plantation, respectively.

Leaves represented the highest proportion of litterfall class among the total litterfall (Figure 2b). The percentage of leaf litter varied among forest types in a range of 60 – 69% of total litterfall production. Mean leaf litterfall in old growth forest was 5.7 t ha^{-1} y^{-1} (95% CI: 4.9 – 6.5), higher than in moderately logged forest by 5.3 t ha^{-1} y^{-1} (95% CI: 4.6 – 6.1) and 4.4 t ha^{-1} y^{-1} (95% CI: 4.0 – 4.8) in heavily logged forest. The oil palm plantation showed the lowest leaf litter (7%) with a total litterfall production of 1.0 t ha^{-1} y^{-1} (95% CI: 0.9 – 1.3). The reproductive parts litter was indistinguishable between sites, but was a mean of 1.02 t ha^{-1} y^{-1} (95% CI: 1 – 1.03) in heavily logged forest, 1.01 t ha^{-1} y^{-1} (95% CI: 0.99 – 1.03) in moderately logged forest and 1 t ha^{-1} y^{-1} (0.98 – 1.02) in old growth forest (Figure 3). Miscellaneous material contributed the second highest proportion to total litterfall production, making up 64% in oil palm, 25% in heavily logged forest, 19% in moderately logged forest and 18% in old growth forest.

C and N concentration

The mean leaf litter C concentration was very similar among sites in the range of 46.97% – 50.21% C per gram of litter, and statistically significant (Figure 4a: $F_{3,13} = 3.3$, $P < 0.05$). Oil palm leaf litter C concentration was 46.97 % (95% CI: 45.15 – 48.87) and lower than mixed leaf litter in forest types. The leaf litter C concentration in forest types was indistinguishable (Figure 4). Leaf litter C concentration in moderately logged forest contained 50.21 % (95%

CI: 48.53 – 51.95), which was very similar than in heavily logged forest of 50%; (48.69 – 51.38) and 49.88%; (48.21 – 51.60) in old growth forest.

Leaf litter N concentration was significantly different between sites (Figure 4b: $F_{3,13} = 18.35$, $P < 0.0001$), and value ranged from 1.51% - 2.16% N per gram of leaf litter. The leaf litter N concentration was very similar among sites. Oil palm plantation contained a higher percentage of leaf litter N by 2.16% (95% CI: 1.98 – 2.36) than leaf mixtures across forest types. Leaf litter N concentration was fairly constant and indistinguishable across forest types (Figure 4): heavily logged forest 1.66 % N (95% CI: 1.57 – 1.76), moderately logged forest of 1.54 % N (1.42 – 1.66)] and old growth forest 1.51 % N (1.39 – 1.62).

The C:N ratio of leaf litter was significantly different between sites (Figure 4c: $F_{3,13} = 25.93$, $P < 0.0001$). The leaf litter C:N ratio in oil palm plantation was 21.72 C:N ratio (19.89 – 23.70); lower than in forests sites. The C:N ratio of mixed leaf litter in forest types was very similar. The leaf litter C:N ratio in heavily logged forest was 30.13 C:N ratio (95% CI: 28.45 – 31.90), increasing to 32.72 C:N ratio (30.38 – 35.25) in moderately logged forest and 33.08 C:N ratio (30.71 – 35.63) in old growth forest.

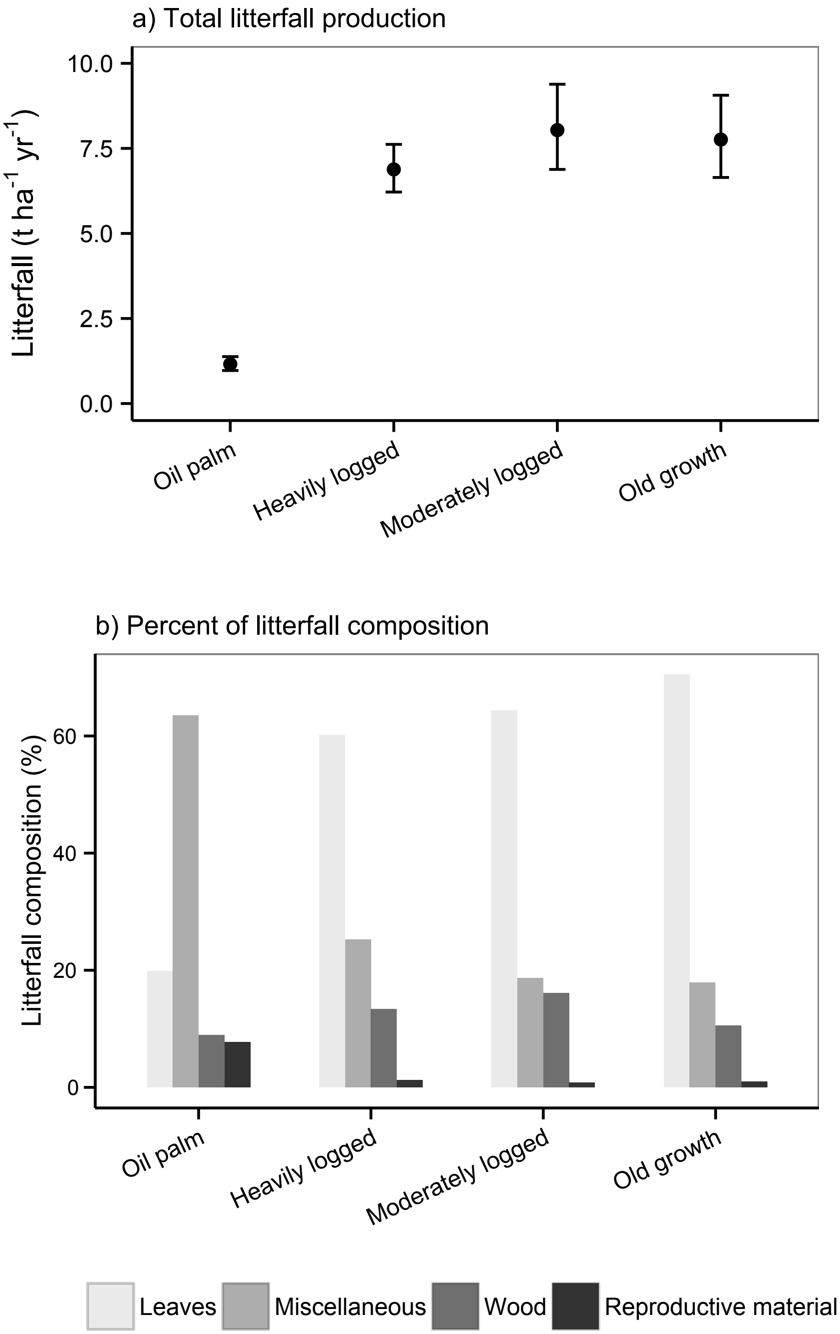

Figure 2: Estimates of annual litterfall production (a) and the components composition (b) in across sites. Black circles represent mean total litterfall production and upper and lower bars 95% CI.

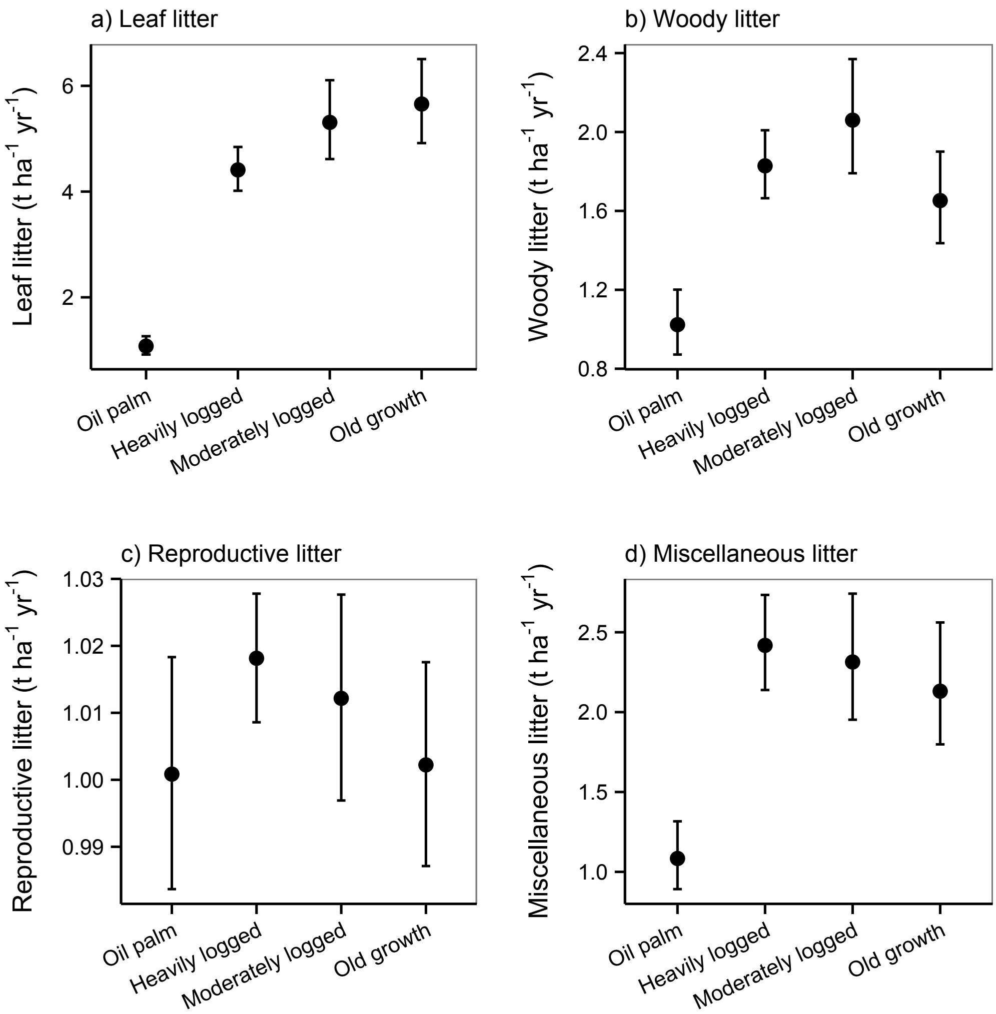

Figure 3: Mean litterfall production for different litter categories across sites. Black circles represent mean total litterfall production and upper and lower bars 95% CI.

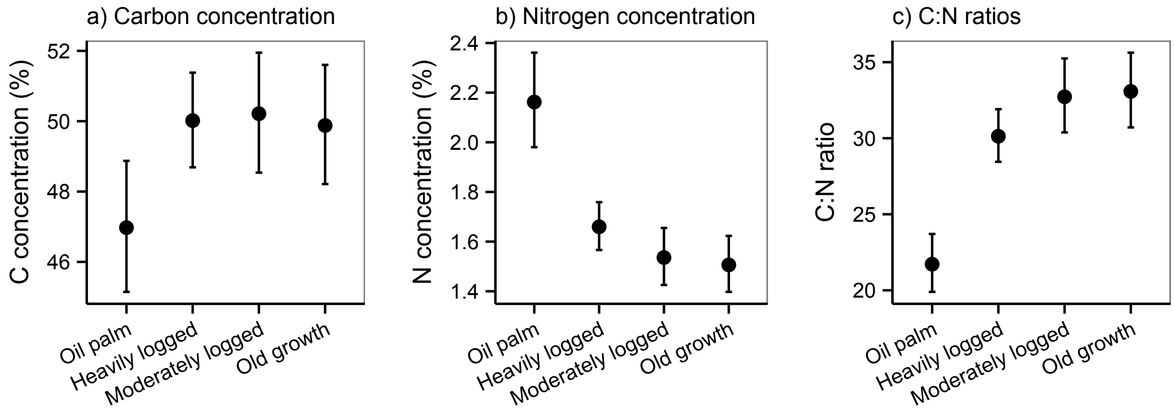

Figure 4: Estimates of mean leaf litter carbon (a) and nitrogen concentration (b), and C:N ratios (c) across sites. Black circles represent mean values with 95% CI.

Discussion

To our knowledge this is the first study to compare litterfall and leaf litter C and N concentration between old growth forest, degraded forest and oil palm habitats. We found that forest degradation had little detectable effect on litter quantity and quality but conversion to oil palm plantation results in a vegetation with lower litter production but litter much richer in N and with a lower C:N ratio.

Litterfall production

We found that litterfall production between old growth forest and degraded forest types were similar and statistically indistinguishable with the sample size and power of this study. However, litterfall production declined sharply after habitat conversion from forest to oil palm (Figure 1a). Indeed, most of the forest habitats were still covered with trees, which represent important resources for litterfall production. We found that the contribution of woody and miscellaneous litter to litterfall production differed between forests sites.

Degraded forest showed a higher contribution of dead branches or deadwood. In contrast, leaf litter contributed a high amount to total litterfall production in old growth forest. These may be explain by a higher canopy and leaf density in old growth forest and higher tree mortality and turnover in degraded forest. Several studies demonstrated that the amount of leaf litterfall production correlated to vegetation species composition (Burghouts et al., 1994) and differences of forest structure (Celentano et al., 2010; Schessl et al., 2008).

The lack of difference in total litterfall production between forest types in this study supported by the results of other studies conducted in tropical regions (Chave et al., 2010; van Schalk and Mirmanto, 1985; Zhang et al., 2014). Most authors found that the environmental variables such as soil, vegetation stand age, species density and diversity have no clear impact on litterfall production. We found that litterfall production ranged from 6.9 to 8.0 t ha^{-1} y^{-1}. This finding is in line with the litterfall levels recorded for forest ecosystems worldwide, which is 3 – 11 t ha^{-1} y^{-1} (Zhang et al., 2014). Litterfall production in this study is very similar to that reported by Dent et al. (2006) in Sepilok Forest Reserve (6.7 – 8.3 t ha^{-1} y^{-1}), slightly lower than that reported by Proctor et al. (1983) in Mulu National Park (8.2 – 9.4 t ha^{-1} y^{-1}), and higher than that reported by Saner et al. (2012) in logged forest (4.9 t ha^{-1} y^{-1}) at Malua Forest Reserve. Litterfall production in this study also higher than that reported by Burghouts et al. (1992) nearby the Danum Valley, which was 6.2 t ha^{-1} y^{-1} in logged forest and 6.6 t ha^{-1} y^{-1} in primary forest. The differences in litterfall production in this study compared with that recorded elsewhere most likely reflects the sampling methodology (Saner et al., 2012) and climate (Zhang et al. 2014). Another study in tropical South America by Chave et al. (2010) found that litterfall seasonality was significantly positively correlated with rainfall seasonality.

Litterfall production in oil palm plantation was a general estimation, due to lack of sampling of oil palm pruned fronds. Aholoukpé et al. (2013) demonstrated that oil palm frond contributed to total biomass stocks in oil palm plantation. This indicated that pruned oil palms fronds may contribute to litter resources, and it should be counted for annual litter production. However, we found that litterfall production in oil palm plantation was 1.15 t ha^{-1} y^{-1} (95% CI: 0.97 – 1.38). Miscellaneous material or unidentified contributed a higher amount to the litterfall production in the oil palm habitat. These may cause by human behavior, where those materials such as soil, rocks and dry branches etc. were placed in the litter trap during maintenance of oil palms and harvesting activities. Leaf litter contributed the second highest amount to total litterfall production. We found that leaves of ferns, grasses, climbers and shrubs were the most collected. Ferns and climbers commonly grow on oil palm trunks. Grasses and shrubs are abundance in the understory of oil palm. A study by Luskin and Potts (2011) found that epiphyte density in young plantations was twice that of old plantations. They found that ferns dominated the epiphytic community, that climbers were the largest but rarest epiphyte and that grasses were the smallest.

Leaf litter C and N concentration

We found that C and N concentration in leaf litter of forest sites were very similar and indistinguishable, and that N concentration was slightly higher in heavily logged forest. These results may correlate with a change of litterfall in heavily logged forests, which are commonly dominated by pioneer species and immature trees. As the C concentration did not significantly differ between forest types, the lower N concentration resulted a higher C:N ratio in old growth forest. The C:N ratio has been used as an index of litter quality, with C:N ratios of < 25 representing higher quality plant tissue, which is more favorable to decomposers, and C:N ratios of > 25 representing low quality plant tissue, which is less favorable to decomposers and slows the decomposition process (Myers et al., 1994). The similarity of C:N ratios between old growth forest and moderately logged forest demonstrates that that selective logging has little effect on litterfall quality. In contrast, the C:N ratio in heavily logged forest was slightly reduced, probably due to differences of forest structure, canopy density and vegetation composition. The change of litterfall quality may impact on soil fertility and regeneration processes in logged forests (Brearley et al., 2003).

A lower concentration of C and an altered C:N ratio in oil palm compare to forest suggests that forest habitat change has reduced the quality of leaf litter. This may be due to a decrease in the species diversity of litter, from many types in forest to only one in oil palm plantation. The higher amount of N in oil palm plantation may indicate use of fertilizer with N to oil palms. The reduction of the C:N ratio in oil palm plantation may effect the nutrient cycling and soil fertility. Therefore, oil palm plantation may have to use additional fertilizer into oil palm plantation to support nutritional needs (Schroth et al., 2006). Although the comparison between forest and oil palm habitat is biased in term of the biophysical characteristics, it non-the-less boosters an existing arguments showing importance of forest reserves in agricultural landscape. As an example, a study by Gray et al. (2014) found that riparian forest reserves alongside rivers in oil palm plantation can support dung beetle biodiversity and may potentially maintain the conservation value of degraded forest reserves. This study shows that such degraded forests may also support forest-type nutrient dynamics.

Conclusion

In conclusion, we found that old growth and degraded forest were similar in terms of litterfall production, litterfall composition, and leaf litter C and N concentration. However, conversion of forest habitats to oil palm significantly reduced litterfall production and changed leaf litter C and N concentrations. This also resulted in a decrease in the C:N ratio, due to the higher N concentrations in oil palm. These may add knowledge on ecosystem functioning to maintain stability of altered forest ecosystems in degraded forest and habitat change especially to improve biodiversity in oil palm habitats.

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CHAPTER 4

Effects of Forest Degradation on Canopy Cover and Seedling Dynamics in Bornean forest

Abstract

Understanding the natural recovery of logged forest is crucial in supporting biodiversity conservation efforts. Logged forests are expected to recover through natural succession but only a handful of studies on the natural recovery following various degree of logging disturbance have been documented. We investigated the effects of forest degradation on the canopy cover and seedling dynamics of unlogged, moderately logged and heavily logged forest. We quantified the vegetation composition, percentage of canopy cover, and seedling basal diameter. We sampled a total of 2,157 seedlings by censuring 0.21 ha areas for the large seedlings and 0.03 ha areas for small seedlings across 84 vegetation plots. The seedlings belonged to 63 families, with Fabaceae, Euphorbiaceae and Annonaceae being among the most recorded in all forest types. The Dipterocarpaceae were dominant in unlogged forest. We found vegetation within the sampling plots differed between forest types. Unlogged forest had the highest tree cover, followed by moderately logged forest and then heavily logged forest with approximately 70%, 54% and 36% cover, respectively. The covers of vines, gingers, shrubs, ferns and grasses were higher in heavily logged forest than moderately logged and unlogged forest. Unlogged forest had the densest canopy cover of approximately 74% (95% CI: 58 – 89) compared to 59% (44 – 74) in the moderately logged and 34% (23 – 44) in heavily logged forest. Seedling density was highest in moderately logged forest (2.53 seedlings per m^2; 95% CI: 1.76 -3.62) followed by unlogged forest (1.82 seedlings per m^2; 1.12 – 3.06) and heavily logged forest (0.85 seedlings per m^2; 0.55 – 1.22). Generally across plots, high quality forest with closed canopy, dense trees with low disturbance had the highest seedling density. Seedling basal diameter size was not significantly different between forest types, but variance components analysis indicated that species identity was important for natural seedling recovery.

Introduction

Exploitation of forest resources and expansion of agricultural activities has caused rapid forest fragmentation and led to a reduction in biodiversity (Koh, 2011; Sodhi et al., 2004; Wilcove et al., 2013). Protection and conservation of tropical forest is key to the maintenance of biodiversity (Sodhi et al., 2009; Wilcove et al., 2013). Although many studies have investigated the structure and compositional of tropical forests, only a few have focused on canopy cover and seedling dynamics, which may change in response to logging intensity. This information is fundamental to understanding what management may be necessary to facilitate the natural recovery of degraded forest.

Natural recovery of disturbed forests is not always possible because of inadequate seed and seedling banks, excessive damage to existing natural vegetation during harvesting, and poor maintenance of existing trees following harvesting (Brown, 2004). Chazdon, 2003 stated that the intensity of disturbance influences the natural recovery process and is often associated with the degree of disturbance and the species composition of remaining forest. The success of natural recovery is also dependent on the level of seed resources and complex interactions between the vegetation community, seed dispersal agents and the environmental conditions (Clark et al., 2001; Webb and Peart, 2001). A low density of remnant trees in degraded forest may lead to a reduction in the natural regeneration process and further species losses. Natural regeneration failure potentially have negative consequences for biodiversity and ecosystem functioning from the local to the global scale (Koh et al., 2013; Sodhi et al., 2010).

Numerous studies have shown that continued logging can cause a reduction in remnant vegetation and can limit natural regeneration process (Nussbaum et al., 1995; Webb and

Peart, 2000; Bischoff et al., 2005). A study by Guariguata and Ostertag, (2001) found that remnant forest vegetation acts as an important seed source during regeneration, which can lead to increased species richness, nutrient availability and aboveground biomass, as well as altering the community composition. Other studies in tropical regions have found that the natural recovery of logged and fragmented forests are affected by disturbance intensity (Pinard and Putz, 1996), soil condition and nutrient levels (Nussbaum et al., 1995), forest composition and structure (Webb and Peart, 2000), size of fragment and distance to the forest fragment edge (Malvido and Ramos, 2003; Vasconcelos and Laurance, 2005).

In Southeast Asia, degraded forest is commonly situated within extensive areas of agriculture (Koh, 2007; Phillips and Lewis, 2013). Conversion of continuous forest reserves to agriculture has been a major caused of a reduction of forest landscape and biodiversity loss in this region (Sodhi et al., 2010). Due to depletion of primary forest, it has increasingly important to understand the successional processes within logged forest ecosystems. Studies of forest recovery indicated that seedling dynamics in different environment following logging disturbance vary in response to seedling growth (Nussbaum et al., 1995), habitat (Webb and Peart, 2000), successional stage (Bischoff et al., 2005), density-dependent predation of seeds (Bagchi et al., 2011) and climate change (Newbery et al., 2011; O'Brien et al., 2013). Furthermore, light-based regeneration niches are important for seedling recruitment (Bebber et al., 2002; Rüger et al., 2009; Whitmore and Brown, 1996) and light heterogeneity in lowland Bornean forest is likely to contribute to the maintenance of Dipterocarpaceae diversity (Philipson et al., 2011).

To our knowledge, most previous studies on forest recovery have concentrated on specific seedling species, and rarely considered natural recovery across disturbance gradients. However, natural seedlings can contribute to the persistence of biodiversity and are key to successional processes and the management of degraded forest. In this study, we investigate the impact of logging intensity on natural forest recovery in forest plots located in Borneo, Sabah, Malaysia. We sampled three forest types: unlogged forest, moderately logged forest and heavily logged forest. We examined the effect of forest degradation on canopy cover, seedling density and seedling basal diameter. We addressed the following key questions: (1) Are logged forest canopies patchier than those in unlogged forest? (2) Does forest degradation reduce seedling densities? (3) Does seedling basal diameter vary among or between species?

Methods

Study area

This study is part of the Stability of Altered Forest Ecosystems (SAFE) Project, which is located in the South-West of Sabah, Borneo, Malaysia (4^{o} 38’ N to 4^{o} 46’ N, 116^{o} 57’ to 117^{o} 42’ E). The SAFE Project area consists of a mixed landscape of oil palm plantation, logged forest and unlogged forest (within the Maliau Basin Conservation Area; Figure 1). The SAFE Project aims to understand the ecological impacts of tropical forest habitat change and fragmentation (Ewers et al., 2011).

Three level of forest disturbance were included in the study: old growth forest, moderately logged forest and heavily logged forest. The unlogged forest was pristine and had never been logged. The moderately logged forest had been logged twice with a selective logging method.

The heavily logged forest had also been logged twice, with the second rotation using a modified selective system. Both moderately logged and heavily logged forests were logged once during the 1970s and a second time from the late 1990s to the early 2000s. The heavily logged forest contained a high density of logging roads, timber stumping areas and skid trails, with only a few commercial and emergent trees remaining and the rest of the community being dominated by pioneer species. The heavily logged forest area had approximately 113 m^3 ha^{-1} of timber removed during the first harvesting rotation and about 66 m^3 ha^{-1} of timber removed during the second rotation (Struebig et al., 2013). This area will be converted to oil palm plantation, creating forest fragments that will be studied by the SAFE Project experiment.

Sampling design

In April 2011, we established 84 seedling plots across eight of the SAFE Project sampling blocks in three forest habitat types. These included two blocks in unlogged forest (OG1 and OG2), two blocks in moderately logged forest (LF1 and LF2) and four blocks in heavily logged forest (A, C, D and E). In total, we established 18 seedling plots in unlogged and moderately logged forest, and 48 plots in heavily logged forest (Table 1). Each seedling plot was setup at the centre of one of the subplots (A) within the SAFE vegetation plot. We established a 5 m^2 plot and a 2 m^2 subplot to measure large and small seedlings, respectively.

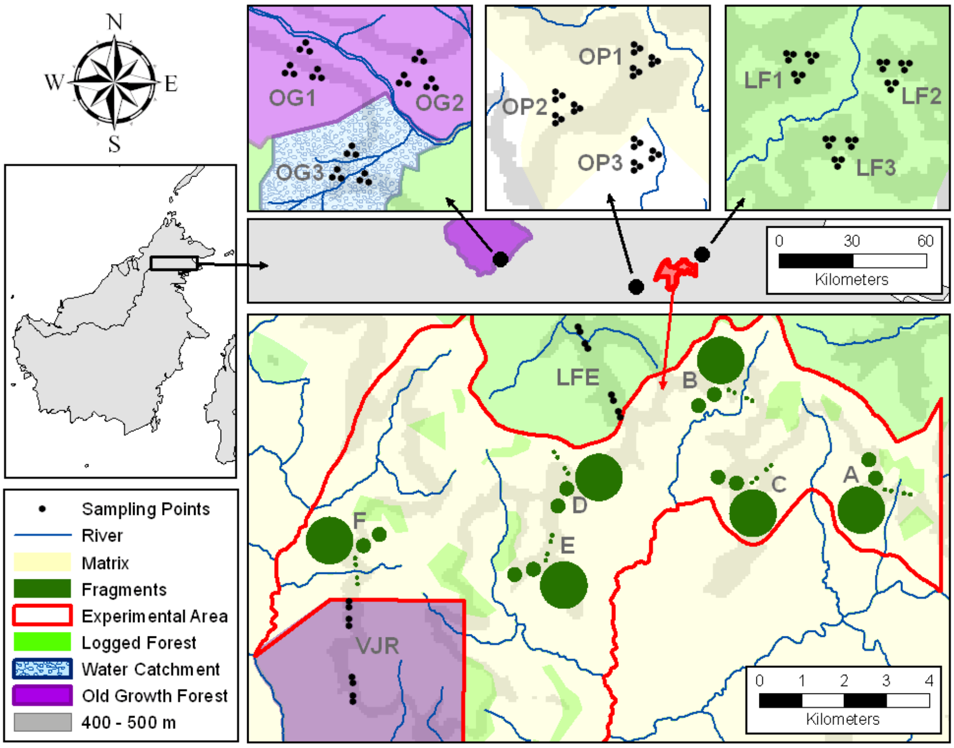

Figure 1: Location map of the SAFE Project study area. Detailed sampling design and plot location can be found in Ewers et al. (2011). Old growth forest blocks of OG1 and OG2 were located within the Maliau Basin Conservation Area, which is located 70 km from the SAFE Project experiment area.

Table 1: Forest descriptions and seedling plot locations in the SAFE Project study area. Block corresponds to the sampling sites illustrated in Figure 1 and is ordered from least to most disturbed (after Ewers *et al.* 2011).

Site	Logging history	Block	Canopy cover (%)	Number of seedling plots	Forest structure
Undisturbed forest	Never	OG1	100	9	Dominated by Dipterocarpaceae species
		OG2	100	9	
Moderately logged forest	Twice	LF1	100	9	Mixed forest
		LF2	86	9	
Highly logged forest	Twice	D	35	12	Mixed forest mostly dominated by pioneer trees
		A	26	12	
		E	21	12	
		C	16	12	

Data collection

In the 5 m^2 plot, all large seedlings of above 50 cm height and less than 1 cm diameter at 1.3 m height were tagged and identified. In the 2 m^2 subplot, all small seedlings with height of between 10 cm and 50 cm, were tagged and identified and their diameter and height recorded. The basal diameter point of measurement (POM) of all seedlings is at 20 cm height from the ground and marked. Two readings (at 90^o to one another) of basal diameter at POM were taken using the digital callipers. An average of these two readings was used for statistics analysis. We also recorded percentages presence of different vegetation types within the larger seedling plots (5 m^2). We classified seven types of vegetation, which included: tree, vine, ginger, shrub, fern, grass and palm. The canopy density was measured at the middle of the seedling plot using the spherical densiometer held at 1.30 m height from the ground. We took four readings to the north, west, south and east, taking an average to calculate the percentages canopy density. We also used forest structure quality classes observed by Ewers et al. (2011), where forest is classed as: (1) very poor, no standing trees, open canopy with ginger, vines or low scrub; (2) poor, open canopy with occasional small trees over a ginger and vine layer; (3) okay, small trees abundant and canopy at least partly closed; (4) good, lots of trees including some large trees and a closed canopy; and (5) very good, no evidence of logging, closed canopy with large trees.

Analysis

We used canopy density to calculate canopy patchiness variation between undisturbed and logged forest. The canopy cover percentages were square root transformed before analysis as they showed a skewed distribution. To test the effect of forest degradation on seedling density, we modelled seedling density as a response variable, with forest quality (n=5) as a fixed effect and block as a random effect (n=8). To meet the assumptions of normality, we log-transformed seedling density data prior to analysis. We then modelled seedling density against forest habitat type (n=3) as a fixed effect and block as a random effect (n=8).

In order to assess the basal diameter size variation among and between blocks, plots and species. To avoid damage of seedling during basal diameter measurement, we only recorded seedlings above 25 cm height and used in this analysis. We modelled seedling basal diameter as a response variable against forest habitat type, as a fixed effect, and block, plot and seedling genera, as random effects. This enabled us to calculate variance components and evaluate different explanatory variables (Hector et al., 2011). We used Linear Mixed-Effects Model (lme) nlme packages from R version 2.15.3 (R Development Core Team 2011) to model the effect of comparison (Crawley, 2012; Pinheiro and Bates, 2009) and present mean estimates with 95% confidence intervals (CI).

Results

Vegetation composition

Trees dominated the vegetation composition across all sites (Figure 2). Unlogged forest had higher tree cover compared to moderately logged forest and heavily logged forest, with an average of 70%, 54% and 36%, respectively. Vines, gingers, shrubs, ferns and grasses were more abundant in heavily logged forest, compared to moderately logged and unlogged forest.

Canopy cover

Canopy cover varied significantly among forest types (Figure 3; $F_{2,5} = 24.64$, $P < 0.003$). Unlogged forest had a greater canopy cover (74%; 95% CI: 58 – 89), than moderately logged forest (59%; 44 – 74) and heavily logged forest (34%; 23 – 44).

Seedling dynamics

A total of 2,157 seedlings, belonging to 63 families, were recorded from 84 plots across the forest types. The relative density of species differed among forest types. Fabaceae, Euphorbiaceae and Annonaceae were recorded in most of forest types. The relative density of Dipterocarpaceae was higher in the unlogged forest (making up 22.6% of individuals), while Fabaceae was higher in both moderately and heavily logged forest (making up16.6% and 17.0% of individuals, respectively) (Table 2).

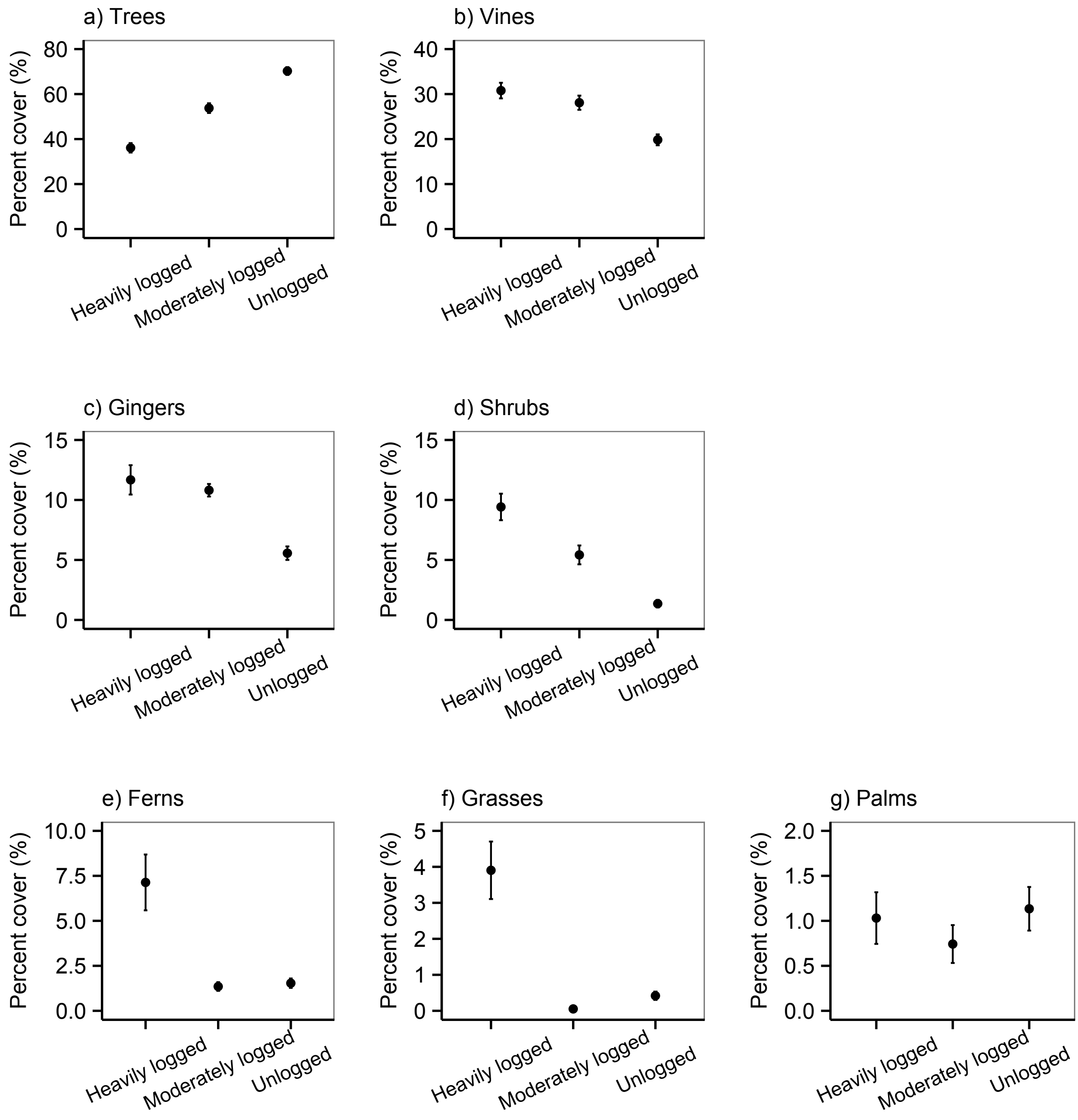

Figure 2: Percent cover of vegetation in plots between forest types. Black circles represent mean percent cover with upper and lower bars 95% CI.

The mean seedling density varied across forest types (Figure 3; $F_{2,5} = 14.51$, $P < 0.008$). Mean seedling density was higher in moderately logged forest (2.53 seedlings per m^2; 95% CI: 1.76 -3.62) but not significantly different from unlogged forest (1.85 seedlings per m^2; 1.12 – 3.06) which were both significantly higher that heavily logged forest (0.85 seedlings per m^2; 0.55 – 1.22).

Tree and vine seedling densities varied among forest types, where moderately logged forest and unlogged forest were more variable and similar than in heavily logged forest (Figure 4). Both large and small seedling densities are generally increasing with lower disturbance. Tree seedling density is more abundance than vine across forest types.

Forest quality varied significantly with seedling density (Figure 5; $F_{4,72} = 5.96$, $P < 0.0003$). Seedling density was highest in good quality forest (2.15 seedlings per m^2; 95% CI: 1.00 – 4.60), followed by very good quality forest (1.90 seedlings per m^2; 1.18 – 3.07), intermediate quality forest (1.68 seedlings per m^2; 1.21 – 2.32), poor quality forest (0.74 seedlings per m^2; 0.47 – 1.15)] and very poor quality forest (0.42 seedlings per m^2; 0.23 – 0.76).

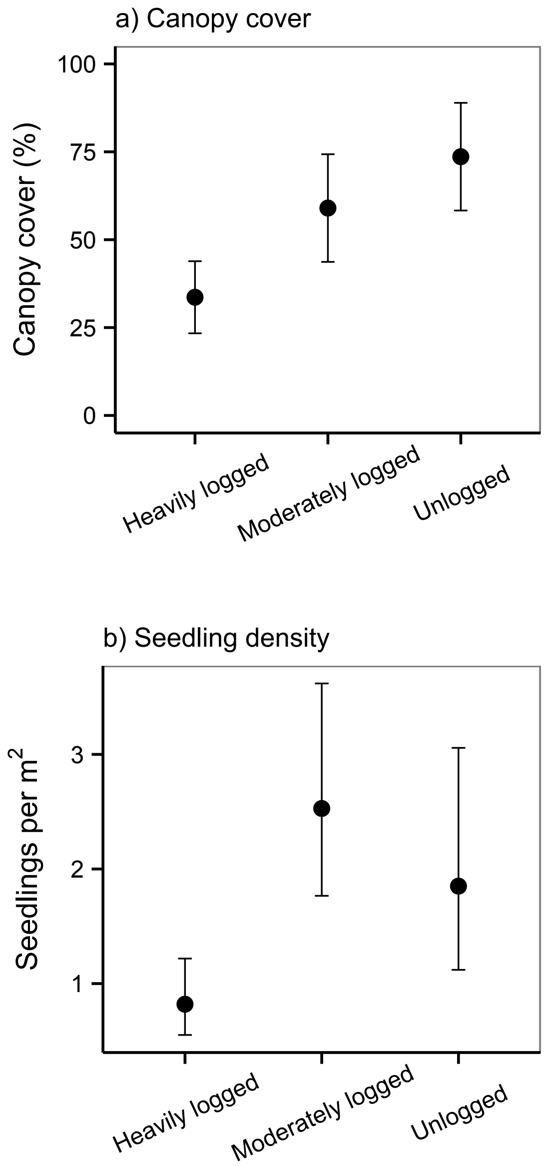

Figure 3: Mean canopy cover (a) and seedling density (b) between different forest types. Black circles represent mean canopy cover and seedling density with upper and lower bars 95% CI. Moderately logged forest had an intermediate canopy cover but a higher seedling density than the other forest types.

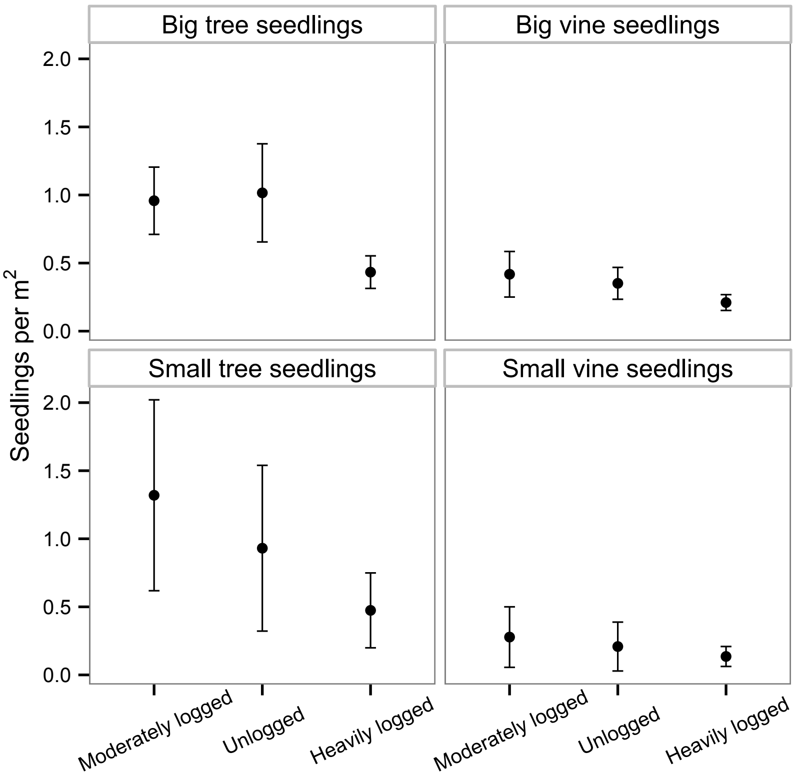

Figure 4: Seedling density of trees and vines in different category by sizes between forest types Black circles represent mean seedling density with upper and lower bars 95% CI.

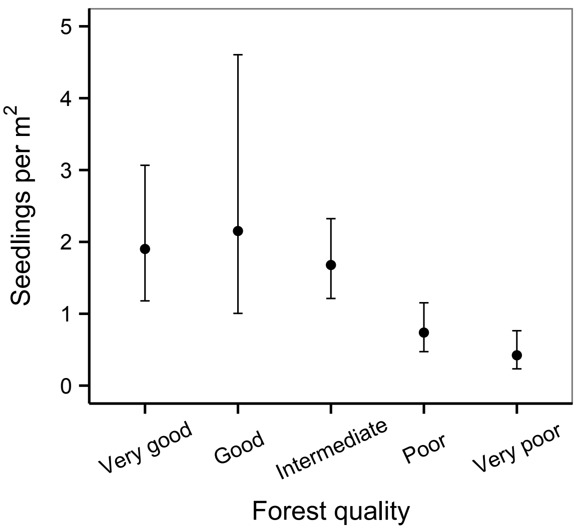

Figure 5: Seedling density in different forest quality across forest types. Black circles represent mean seedling density with upper and lower bars 95% CI.

Seedling basal diameter

A total of 2008 seedlings of 25 cm height from the ground and above were analysed to assess how basal diameter varied with forest types. We found that seedling basal diameter size did not very significantly between forest types (Figure 6; $F_{2,5} = 3.81$, $P < 0.09$). The mean sizes of seedling basal diameter in heavily logged forest was 8.96 mm (95% CI: 8.15 – 9.87), which was slightly higher than in the undisturbed forest and moderate logged forest with 7.8 mm (6.93 – 8.91) and 7.7 mm (6.80 – 8.78), respectively. The standard deviation (SD) variance components of seedling basal diameter varied among explanatory variables, with species identity (0.25 SD; 95% CI: 0.22 – 0.30) being more significant and explained more than plot (0.09 SD; 0.05 – 0.15) and block (0.05 SD; 0.01 – 0.17). The variance components of plot and block were similar (Figure 7). This indicates that species identity is more important than spatial variability in determining the success of natural recovery.

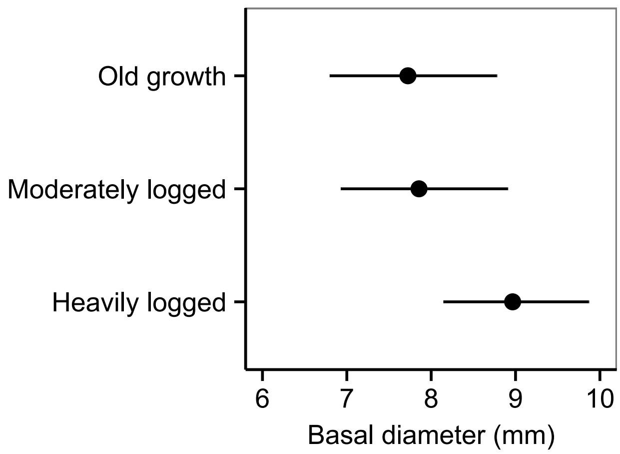

Figure 6: Seedling basal diameter between forest types. Black circles represent mean seedling basal diameter with upper and lower bars 95% CI.

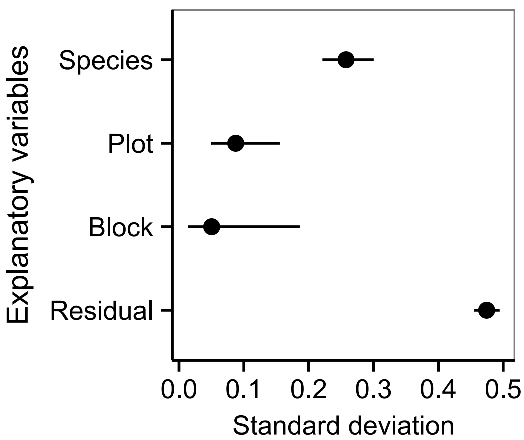

Figure 7: The variance components analysis of seedling basal diameter across study sites. Black circles represent standard deviation of explanatory variables with upper and lower bars 95% CI.

Discussion

Studies on logged forests are important for assessing the effects of forest degradation and for informing tropical biodiversity conservation efforts. We surveyed old growth forest, moderately logged forest and heavily logged forest to determine whether degradation affected canopy cover, seedling density and seedling basal diameter. We found a significantly effect of forest degradation to canopy cover (Figure 3a) and vegetation cover (Figure 2) across forest types. Forest degradation caused a reduction in seedling density from old growth forest to heavily logged forest but not to moderately logged forest (Figure 3). Seedlings basal diameter sizes a very similar between forest types (Figure 6). Species identity was identified as an important explanatory variable in determining natural succession following forest degradation (Figure 7).

Effect of forest degradation on canopy cover and vegetation composition

Forest degradation reduced canopy cover and increased vegetation composition of vines, gingers, shrubs, ferns and grasses (Figure 2, Figure 3). As expected, canopy cover was higher in unlogged forest and lower in logged forest. The lowest canopy cover was observed in heavily logged forest. This was probably due to the fact that most of the large trees with emergent canopies were removed during logging. In contrast, large trees and emergent canopy still present in unlogged forest. A similar trend for low canopy cover in logged forests were reported elsewhere in the tropics (Asner et al., 2009; Pereira et al., 2002; Woods, 1989). As an example, Pereira et al. (2002) found that canopy gap fraction in recently logged areas using reduced-impact logging and conventional was 22% and 11% of the total area, respectively.

This suggests that canopy cover in logged forests is dependent on logging intensity and timber extracted, which is related to the logging practices (Barone et al. 1997). Similar results have also been reported for other studies in Bornean forests, where the structure of logged forest has been found to be influenced by logging techniques (Bertault and Sist, 1997; Saner et al., 2012; Sist and Bertault, 1998; Tangki and Chappell, 2008; Uuttera et al., 2000). A study conducted by Pinard et al. (2000) indicated that low intensity logging, using reduced impact logging guidelines, reduced damage from 28% to 50% of the original stems.

Both large and small vine and tree seedling abundance differed between forest types. Vegetation composition also varied among forest types, with percentage tree cover being higher in unlogged than in logged forest. Trees cover in unlogged forest was 20% and 40% higher than in moderately logged and heavily logged forest, respectively. These differences are reflected by reductions in recruitment of trees but increases in cover of vines, gingers and herbaceous vegetation (i.e. shrubs, ferns and grasses) in logged forest compared to unlogged forest. In contrast, the cover of palms is similar across forest types. We also observed a positive relationship between logging intensity and non-tree vegetation cover. Forest degradation seems to be facilitating a reduction in canopy cover, creating canopy gaps, which promote the growth of herbaceous vegetation (Figure 2). In contrast dense canopy cover in unlogged forest seems to supress the herbaceous vegetation. These findings are backed up by the results of studies from elsewhere in the tropics, where forest gaps and early successional forests have enhanced recruitment of pioneer species and non-tree species, such vines and herbaceous plants (Duncan and Chapman, 2003; Park et al., 2005; Schnitzer and Carson, 2001).

Effect of forest degradation on seedling dynamics

Seedling density seems to be affected by the volume and density of vegetation removed and damage inflicted to habitats during logging. Seedling density generally declined as forest quality declined (Figure 4). We also found that forest with no standing trees, an open canopy and forest dominated by herbaceous vegetation had lower seedling densities. Similar results have been reported by Li et al. (1999), who found that shrubs inhibited tree growth in older subtropical successional forests. Another study by Capers et al. (2005) in Costa Rica found that light availability was positively correlated to recruitment rates of palms, shrubs and vines.

There was no significant difference in seedling density between unlogged forest and moderately logged forest (Figure 3). However, seedling density was significantly lower in heavily logged forest. These results could help to explain some of the impacts of high logging intensity on natural forest recovery and also to inform management to aid forest regeneration. In particular, the similarity of seedling density in high and medium quality forest indicates that logged forest areas can still act as potential seed sources to enhance natural seed dispersal and facilitate forest recovery in degraded landscapes.

The highest seedlings densities of Dipterocarpaceae species in unlogged forest. This may relect the removal of high timber value Dipterocarpaceae species during logging in moderately logged and heavily logged forest. Previous logging probably reduced stands of mature Dipterocarpaceae trees and consequently limited the seed sources and caused decline of Dipterocarpaceae seedling in logged forests (see Appendix). In contrast, seedling species of Fabaceae, Euphorbiaceae and Annonaceae were found to be abundant in both logged forest, presumably because adults form these groups are less commonly removed during logging. Interestingly, seedling species of Moraceae was found to be the highest in heavily logged forest, which generally indicates abundance of pioneer tree species, shrubs and vines. Most species of shrubs and vines, which has been found in both logged forest not found in unlogged forest. These attributes may be reflecting to the early recovery from logging disturbance, where both logged forest in this study was logging in late 1990s to the early 2000s. The seedlings species composition in unlogged forest was close to that observed by Newbery et al. (1996) at Danum Valley. However, they found that Euphorbiaceae made up the highest density of seedlings, with Dipterocarpaceae second.

We observed no significant difference in seedling basal diameter between forest types. These may be partially due to the method used, where we average basal diameter without considering the species identity. Generally, size of seedling basal diameter in heavily logged does show slightly bigger that in other forest types. This could reflect the faster growth of vines and herbaceous species, which are found more common in heavily logged forest. This is also likely to be the reason why species identity was important in the natural recovery assessment. The attributes of seedling dynamics in this study may suggest that logged forest succession is often inhibited by seed resources, canopy cover and logging disturbance intensity.

Conclusion

Natural forest successions in logged forests have been influenced by damage inflicted during logging activities. However, active management probably able to speed this up and encourage forest regeneration. Numerous studies have found that restoration in logged forest can help maintain and restore forest composition (Ådjers et al., 1995; Shono et al., 2006). In this study, we found that natural recovery processes might be influenced by harvesting intensity. The moderately logged forest that generally showed high to medium percentage canopy cover still supported shade-tolerant tree species. These could potentially promote succession and recovery to old growth forest. In contrast, heavily logged forest with a very low percentage canopy cover, have few tree seedlings present, which may arrest natural succession and slow the recovery process. As a result, with heavy logging, restoration via enrichment planting may be the most appropriate forest management. In contrast, moderately logged forest could be allowed to regenerate naturally from the seedling bank. Long-term monitoring is needed to find out more about how natural recovery changes seedling density and composition over time.

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Appendix

Table showing a list of seedlings family and relative density across forest types

No	Plant Families	Seedling relative density (%)*		
		Old growth	Moderate logged	Heavily logged
1	Achariaceae	0.31	1.31	0.37
2	Actinidiaceae	0.15	0.58	1.22
3	Alangiaceae	0.62	0.73	0.12
4	Anacardiaceae	1.08	1.02	4.38
5	Anisophylleaceae	0.00	0.15	0.00
6	Annacardiaceae	0.00	0.29	0.00
7	Annonaceae	8.15	5.98	5.72
8	Apocynaceae	0.00	0.15	0.00
9	Asteraceae	0.00	0.15	0.00
10	Barringtoniaceae	0.46	0.29	0.00
11	Burseraceae	0.46	1.02	0.37
12	Caesalpiniaceae	2.15	0.87	0.49
13	Celastraceae	0.31	1.90	0.37
14	Chrysobalanaceae	0.31	0.00	0.00
15	Clusiaceae	1.08	0.00	0.00
16	Combretaceae	0.46	1.46	1.10
17	Connaraceae	2.46	4.37	3.29
18	Convolvulaceae	0.00	0.29	1.10
19	Crypteroniaceae	0.00	0.15	0.73
20	Cucurbitaceae	0.00	0.00	0.12
21	Dilleniaceae	0.77	4.52	2.80
22	Dioscoreaceae	0.00	0.00	0.49
23	Dipterocarpaceae	22.62	1.90	3.53
24	Ebenaceae	3.85	3.06	2.56
25	Elaeocarpaceae	0.00	0.15	0.00
26	Euphorbiaceae	17.08	12.24	6.94
27	Fabaceae	13.69	16.62	17.05
28	Fagaceae	0.00	0.44	0.49
29	Icacinaceae	0.62	0.58	0.61
30	Lamiaceae	0.46	2.19	3.90
31	Lauraceae	2.92	2.04	3.05
32	Leeaceae	0.00	0.15	3.17
33	Loganiaceae	0.31	0.44	0.12
34	Lomariopsidaceae	0.15	0.00	0.00
35	Longaniaceae	0.00	0.15	0.00
36	Maesaceae	0.46	0.00	0.00
37	Magnoliaceae	0.00	0.15	0.00
38	Malvaceae	3.08	1.46	0.61
39	Meliaceae	3.54	4.96	1.83

No	Family	Seedling relative density*		
		Old growth	Moderate logged	Heavily logged
40	Moraceae	1.54	2.33	11.81
41	Myristicaceae	0.77	0.29	0.37
42	Myrsinaceae	0.92	0.58	0.73
43	Myrtaceae	0.77	2.19	0.49
44	Oleaceae	0.31	0.73	0.97
45	Polygalaceae	0.46	1.02	0.37
46	Proteaceae	0.00	0.44	0.00
47	Rhamnaceae	0.00	1.90	0.73
48	Rosaceae	0.15	0.15	0.24
49	Rubiaceae	1.54	6.27	2.56
50	Rutaceae	0.00	1.02	1.71
51	Sabiaceae	0.00	0.29	0.00
52	Sapindaceae	0.77	2.04	0.73
53	Sapotaceae	0.62	0.29	0.00
54	Simaroubaceae	0.46	0.00	0.85
55	Smilacaceae	0.00	0.00	0.24
56	Sterculiaceae	0.31	0.87	4.87
57	Symplocaceae	0.00	0.44	0.24
58	Theaceae	0.31	0.15	0.12
59	Thymelaeaceae	0.00	0.29	0.00
60	Ulmaceae	0.00	1.31	0.00
61	Urticaceae	0.00	0.00	1.95
62	Violaceae	0.00	0.29	0.12
63	Vitaceae	0.15	1.46	0.61
64	Unknown	3.38	3.94	3.78

* The percentage of individual seedling family out of the total number of seedlings in forest habitat.

CHAPTER 5

General Discussion

Introduction

Tropical forest habitat change has accelerated as agriculture has expanded, rapidly the changing forest landscapes and reducing of global biodiversity. Active guidelines for management are urgently needed to maintain and enhance biodiversity in both degraded forest and agricultural areas. In forest habitat, sustainable forest management through selective harvesting and reduced impact logging techniques have been identified as an appropriate practices to support the recovery of forest vegetation structure (Imai et al., 2012; Okuda et al., 2003; Villela et al., 2006).

The question of how the integration of forest habitats and agriculture landscapes may support the biodiversity has increased interest to ecologists and conservationists. The issues of land sparing versus land sharing and particularly to understand the fundamental knowledge on how to limit the impact of land use change on biodiversity in future is a fundamental topic. Although studies on forest ecology and biodiversity losses have conducted over the last few decades, there are many issues within biodiversity conservation that are as yet unresolved. The complexity of forest ecosystems, creates far too many gaps in our current knowledge, suggesting more work needs to be carried out to fully understand the consequences of forest degradation and habitat change on biodiversity and ecosystem functioning.

In this thesis, we examine the effects of forest degradation and forest habitat change to oil palm plantations on vegetation structure and ecosystem functioning. we sampled four sites of old growth forest, moderate logged forest, heavily logged forest and oil palm plantation. The main focus of this study between sites are: (Chapter 1) to determine vegetation structure based on tree density, basal area, stock of coarse woody debris (CWD) and total aboveground carbon (TAGC) stocks; (Chapter 2) to evaluate litter production and leaf litter carbon (C) and nitrogen (N) concentration; and (Chapter 3) to examine the responses of forest degradation on seedlings dynamics.

In this chapter, we discuss main findings of this thesis. Firstly, the dynamics of vegetation structure and carbon stocks across sites. Secondly, the pattern of litterfall production and leaf litter C and N concentration across sites. Thirdly, the dynamics of forest structure and seedlings across forest types. Finally, we elaborate on potential approaches to the management of degraded forests and oil palm plantations towards the support of biodiversity conservation and ecosystem functioning.

Vegetation structure and carbon dynamics

We observed that forest degradation and habitat conversion changed the vegetation structure and carbon dynamics across sites (Chapter 2). Forest degradation caused a decline in tree density, basal area, canopy cover and carbon stocks indicating that the removal of big trees and the resulting damage to the surrounding vegetation during logging, influenced the pattern of vegetation structure. Furthermore, the highest logging intensity produced the lowest tree density, basal area and carbon stocks.

Not surprisingly, the change of vegetation structure was strongly related to the amount of timber extracted during logging. For example, both of moderately logged forest and heavily logged forest had been logged twice, however due to difference in logging intensity both sites had a different vegetation structure. The tree density and basal area in moderately logged forest is 67% and 57% higher than in heavily logged forest. The aboveground carbon stock in oil palm habitat is only 3%, 6% and 10% compared to old growth forest, moderately logged forest and heavily logged forest, respectively. The reduction amount of aboveground carbon stocks due to oil palm conversion similarly reported in previous studies by Morel et al. (2011) and Adachi et al. (2011).

Although total coarse woody debris (CWD) stock was statistically indistinguishable across sites, we found that CWD composition of fallen trunks, standing deadwood, hanging trunks and stumps varied among sites. This variation may be an indication of the level of forest degradation. The CWD composition of standing deadwood and stumps was significantly difference between old growth forest and heavily logged forest, but not for moderately logged forest. After second logging rotation, moderately logged forest which has been logged using selective harvesting system left an abundance remnant of forest vegetation compared to heavily logged forest. Vegetation communities in logged forest habitats continue to produce CWD in contrast to oil palm habitats. The significant negative effect of logging on CWD stocks is well established and has been demonstrated in a number of forest ecological studies (Gale, 2000; Keller et al., 2004; Ngo et al., 2013; Saner et al., 2012). As expected, the conversion of forest to oil palm plantation reduced carbon storage. We found a 58% reduction of CWD carbon stocks and in oil palm plantations in contrast to old growth forest.

The positive correlation between total aboveground carbon (TAGC) stocks and basal area across forest types is most likely a result of the positive relationship between the number and sizes of trees to carbon stocks (Stephenson et al., 2014). Conversion of forest habitat to oil palm plantations has a large negative effect on TAGC stocks. We found that TAGC stocks in old growth forest was 132.72 Mg C ha^{-1} (95% CI: 84.68 - 208.46), 70.91 Mg C ha^{-1} (44.60 - 113.12) in moderately logged forest and 46.36 Mg C ha^{-1} (32.72 - 64.87) in heavily logged forest and 10.85 Mg C ha^{-1} (5.93 - 19.92) in oil palm plantation. The reduction of TAGC stocks was 53% in moderately logged forest, 65% in heavily logged forest and 92% in oil palm plantation in contrast to old growth forest. This may just be a general estimate but it potentially evidence of a downturn in ecosystem services due to forest degradation by conversion to oil palm habitat. However, only long-term studies will be able to elucidate if the change of vegetation structure and carbon dynamics from forest to oil palm habitat has a permanent negative impact on ecosystem functioning.

Litterfall production and leaf litter C:N concentration

We found that litterfall production between forest types was statistically indistinguishable. The weak but significant correlation between forest types and litterfall production may be influenced by vegetation structure after logging as discussed in Chapter 3. This could be further influenced by the limitations of our dataset with regard to local biological mechanisms. Other studies in tropical regions found that litterfall production was affected by the gradient of soil nutrient availability (Chave et al., 2010; Dent et al., 2006), vegetation structure and climate (Vitousek, 1984; Zhang et al., 2014)

Heavily logged forests produced the lowest amount of litterfall in contrast to moderately logged forest and old growth forest. Ifound that litterfall production in moderately logged forest was 8.04 t ha^{-1} y^{-1} (95% CI: 6.88 – 9.39), 7.76 t ha^{-1} y^{-1} (6.64 – 9.06) in old growth forest and 6.88 t ha^{-1} y^{-1} (6.23 – 7.62) in heavily logged forest. These observations raise the question as to why there are differences in litterfall production in moderately logged forest and heavily logged forest. This pattern may be in response to canopy cover at different logging intensities and species heterogeneity (Burghouts et al., 1994). The variance of litterfall produced by the forest types in our study compared to other studies elsewhere in the tropics may only be determined after long term monitoring. Meanwhile, we observed that litterfall production ranged between 6.9 and 8.0 t ha^{-1} y^{-1}, comparative to litterfall recorded in forest ecosystems worldwide of 3 – 11 t ha^{-1} y^{-1} (Zhang et al., 2014). In contrast, the litterfall production in oil palm habitat was significantly different to all the forest types in our study. The litterfall production in oil palm plantation was the lowest (1.15 t ha^{-1} y^{-1}; 95% CI: 0.97 – 1.38). Further work is needed to produce a better estimate of leaf litter production in oil palm plantation due to the influence of pruning activities on oil palm fronds during oil palm bunch harvesting (Aholoukpé et al., 2013).

The leaf litter carbon (C) and nitrogen (N) concentration and C:N ratio across forest types was statistically indistinguishable. These observations suggest that leaf litter of mixed species across forest types were consistent and not strongly affected by logging. However, we found that C:N ratio in heavily logged forest slightly decreased compared to moderately logged forest and old growth forest suggesting high logging intensity changed the vegetation structure and effect the leaf litter C:N ratio quality. The pattern of C:N ratio in forest types may be further influenced by vegetation heterogeneity, which changes according to succession species in its home range.

In contrast, oil palm leaves had a lower C:N ratio compared to leaves of the forest types, which was influenced by high N concentration in oil palm leaves. This high N concentration may be a result of N fertilization in the oil palm plantation (Law et al., 2012; Schroth et al., 2006). This findings presented in this study provide a general understanding on litterfall production and leaf litter C and N concentration and C:N ratio of different forest types and oil palm plantation. Further research to increase our knowledge on the effects of forest degradation and habitat change are needed. Furthermore, such knowledge this is crucial to better understand the importance of species composition on nutrient mineralization.

Forest canopy and seedling dynamics

We found that logging has decreased the canopy cover and to a lesser degree seedling density (Chapter 4). These provides additional knowledge on natural recovery trend, where logging intensity has resulted in significant changes in canopy cover, the plant community and seedling density. High logging intensity led to decreased canopy cover in heavily logged forest resulting in changes in forest quality and was significantly positive correlated to the abundance of seedling density. A very poor forest quality, with no standing tree and open canopy with ginger, vines and low scrub showed a decline in seedling density. The findings presented in this study suggest therefore that a decrease in canopy cover provided an appropriate habitat for the growth of vines and herbaceous plants.

We observed that seedlings species of Dipterocarpaceae was the most affected by logging across forest types. Several pioneer seedlings species are widely distributed across logged forest, are not present in old growth forest. The complexity of interactions between canopy cover and species attributes may be an important determining factor in the abundance and dominance of species in logged forest (Okuda et al., 2003). We found that seedlings of Fabaceae, Euphorbiaceae and Annonaceae were abundant species in logged forests and among the most common species in unlogged forest (Bischoff et al., 2005; Newbery et al., 1996).

The study findings suggest that logging changes the species composition of forests. We found species of vegetation species were an important factor in correlation between seedling basal diameter and logging intensity. The importance of the vegetation species has been demonstrated in several studies elsewhere in Southeast Asian forests in which the species of seedlings influenced natural recovery (Imai et al., 2012; Okuda et al., 2003; Verburg and van Eijk-Bos, 2003). The recovery of each species groups differed and was dependent on the intensity of forest distrubance. The influences of canopy cover and light penetration to the forest floor affected the success of seedling growth (Bebber et al., 2002; Philipson et al., 2011). In order to understand the importance of logged forest on maintaining the tree species diversity, a more detail investigation is needed specifically to determine how many and which species are able to persist in logged forests, which in time may become part of the species composition in old growth forest. We suggest that further studies should focus on the recovery of tree species seedlings within oil palm habitats. The natural recovery and survival of tree communities in oil palm habitat may provide the knowledge for the integration of trees into oil palm plantations.

Implications for management of degraded forest and oil palm plantation.

Understanding biodiversity management and ecosystem functioning in degraded forest and in oil palm plantation has encouraged ecologist to broaden their research interests. Several authors have noted that the conversion of forest habitat to oil palm plantations has drastically reduced biodiversity (Butler and Laurance, 2009; Koh and Wilcove, 2008; Wilcove and Koh, 2010). There is evidence to suggest however that preserving some forest habitat within oil palm plantation supported the biodiversity conservation in oil palm development (Foster et al., 2011; Gray et al., 2014; Koh, 2008). As an example, a study by Gray et al. (2014) on degraded forests in a human modified landscape found that forest habitat in oil palm plantation through riparian reserve has provided an opportunity to support dung beetle biodiversity and ecosystem services.

We suggest that protecting the old growth forest and degraded forest is the best approach to support the biodiversity conservation, although there may be some, opportunities to increase biodiversity in oil palm plantations. However, we propose: (1) commercial forests should be managed sustainably through harvesting techniques and diameter cutting limit. In addition, controlling the volume of timber extracted may be a potential approach to optimize timber production and reduce residual damage; (2) appropriate design of oil palm plantation through increased restriction of forest habitat conversion to oil palm plantation especially in areas of high conservation value should be implemented and undergo the environmental impact assessment; and (3) existing oil palm plantations may consider re-establishing forest habitats through by replanting of forest species within the plantation area such as in riparian areas and steep terrain.

In addition, the design of oil palm plantation landscapes should be considered to minimize impact on biodiversity (Koh et al., 2009). Luskin and Potts, (2011) suggested several methods for designing oil palm landscapes which may create temporal scales associated with the oil palm lifecycle. These methods are related to variable retention rotations, reduced field size and altered planting. Furthermore, the issues of damage caused by farming to nature areas implies that future research must address questions such as: (1) what is the scale of demand on food and agricultural production in future, (2) what types of crops and level of production that potentially threaten to nature ecosystems, and (3) what are promising approaches and techniques will be provide better environmental performance on the farming expansion (Balmford et al., 2012; Green et al., 2005). The land-sharing (integration) versus land-sparing (separation) question has been widely debated to determine the most appropriate method for biodiversity protection within timber production and agricultural landscapes (Edwards et al., 2014; Fischer et al., 2014; Rey Benayas and Bullock, 2012). As an example, a study by Edwards et al. (2014) comparing the abundance and species richness of bird, dung beetles and ants in logged forests in Borneo found that within each taxonomic groups, more species had higher abundances with land-sparing in contrast to land-sharing logging.

To support the persistence biodiversity and ecosystem functioning in degraded forests, improvements in harvesting operations and management are needed. Those may include aspects such as: (1) setup of large and continuous logging areas to minimized the edge effect on species dynamics; (2) logging rotation periods to maximized timber volumes and increase the benefits of forest ecosystem function; and (3) excluding a number of mature stands from logging to provide a seed bank for natural recovery.

Furthermore, the choice of restoration management systems in degraded forest areas can be strongly influenced by the remnant stands which provide the seed resources. We found that the high logging intensity of heavily logged forest resulted in an open canopy and enhanced the recruitment of understory vegetation (vines, shrubs and herbaceous plants). This resulted in a large reduction in tree vegetation structure and seedling density in contrast to moderately logged forest and old growth forest. Therefore, successful management to restore the open canopy forest areas may require active maintenance such as weeding and silvicultural treatments. In addition, enrichment planting with shade-intolerant species in open canopy may be appropriate to increase vegetation diversity and to maintain the stability of altered forest ecosystem in degraded forests.

Conclusion

Our findings provide an important contribution to current knowledge for the conservation of biodiversity and ecosystem functions in degraded forests. We show that logging and forest habitat conversion to oil palm plantation leads to a decrease in tree basal area and total aboveground carbon stocks (Chapter 2), reduced litterfall production and degraded the C and N concentration in leaf litter (Chapter 3). In addition, high logging intensity reduced canopy cover and increasing the growth of vines and herbaceous plants which reduced tree seedling density (Chapter 4). Our findings imply there are limitations in the capability of degraded forests and oil palm habitats to support the persistent biodiversity and ecosystem functioning. Moderately degraded forest is better able to maintain ecosystem functioning and provide a habitat for many species of animals, avifauna, insects and other groups. The degraded forest habitats commonly become valuable buffers to old growth forest areas.

This study demonstrated that degraded forests plays an important role in terms of their ability to rapidly restore different vegetation structural and functional aspects similar to old growth forest in contrast to oil palm plantations. The conversion of degraded forests to oil palm plantation has resulted in a decline ecosystem functioning particularly for TAGC stocks. To minimize biodiversity loss and support ecosystem functioning, we suggest therefore that (1) conservation efforts should continue to reduce deforestation for agriculture expansion, (2) conversion to oil palm plantation could minimize impacts on biodiversity by focusing the most degraded forest areas, (3) conversion to oil palm plantation must consider the high conservation value of areas by implementing environmental impact assessments, and (4) reserves of forest habitat within oil palm plantation areas should be implemented by avoiding planting of oil palms at least in riparian areas and steep terrain. Whereas biodiversity in oil palm plantation is impossible to compare to biodiversity within forest habitats, design of landscape and careful planning may increase biodiversity in oil palm plantations. Moreover, forest managers should enforce forest sustainable practices and implement restoration on degraded forest to maintain the stability of altered forest ecosystems. Further studies are still need to determine if the forest degradation and conversion to oil palm plantation will permanently impact ecosystem functioning. Indeed, continuous monitoring is required to evaluate the success of biodiversity conservation and ecosystem functioning in integrated landscapes of oil palm plantations and forest habitats.

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